



Strukturen i en muslingebanke og dennes betydning for blåmuslingers vækst og dødelighed

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STRUKTUREN I EN MUSLINGEBANKE OG DENNES BETYDNING FOR BLÅMUSLINGERS VÆKST OG DØDELIGHED.

Ph.D. afhandling 1998



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Forord

Denne Ph.D.-afhandling præsenterer et studie af strukturen i muslingebanker. Det blev påbegyndt i 1992-1993, da jeg var NKMB-stipendiat på Kristineberg Marinbiologiske Station i Sverige med Dr. Ib Svane som vejleder. I 1994 blev jeg ansat ved Danmarks Fiskeri- og Havundersøgelser og blev optaget som Ph.D.-studerende ved Københavns Universitet med Professor Tom Fenchel, Marinbiologisk Laboratorium, Helsingør som vejleder.

Mange mennesker har undervejs hjulpet mig, og gjort dette studie muligt. Først af alle vil jeg takke Dr. Ib Svane, Kristineberg Marine Forskningsstation (KMF), der introducerede mig til de spændende problemstillinger om blåmuslingernes bankestrukturer, og som både har været en god lærmester i eksperimentelle feltundersøgelser og en inspirerende samarbejdspartner. Desuden vil jeg takke Professor J.-O. Strömberg og personalet på KMF for hjælp i det år, jeg var stipendiat. Ligeledes vil jeg takke alle mine kolleger ved DFU, Afdeling for Havfiskeri, der har givet mig mulighed for at bruge det meste af min arbejdstid til dette studie. Erik Hoffmann og Per Sand Kristensen har givet mig en god introduktion til Limfjordens blåmuslinge-fiskeri og Alex Hansen, Nina Holm, Agnete Hedegaard, Palle Brogård og Niels Jørgen Pihl takkes for hjælp i forbindelse med feltundersøgelser og dataoparbejdning. Jeg vil takke Prof. Tom Fenchel for vejledning og råd i forbindelse med Ph.D.-projektets gennemførsel.

Endelig vil jeg takke min familie for deres interesse i mit arbejde.

Charlottenlund Slot, maj 1998

Per Dolmer

Følgende artikler indgår i denne rapport og vil blive refereret til med deres nummer:

- I. Dolmer, P. The structure of *Mytilus edulis* beds: effects of small-scale seston distribution. - Manuskript.
- II. Dolmer, P. & I. Svane. 1994. Attachment and orientation of *Mytilus edulis* L. in flowing water. - *Ophelia* 40: 63-74.
- III. Dolmer, P., M. Karlsson & I. Svane. 1994. A test of rheotactic behaviour of the blue mussel *Mytilus edulis* L. - *Phuket Mar. Biol. Cent. Spec. Publ.* 13: 177-184.
- IV. Dolmer, P. Seasonal and spatial variability in growth of *Mytilus edulis* L. in a brackish sound: comparisons of individual mussel growth and growth of size classes. - Accepteret af Fisheries Research.
- V. Dolmer, P. The interactions between bed structure of *Mytilus edulis* L. and the predator *Asterias rubens* L. - Accepteret af J. Exp. Mar. Biol. Ecol.
- VI. Dolmer, P.; P. S. Kristensen og E. Hoffmann. Dredging of blue mussels (*Mytilus edulis* L.) in a Danish sound: estimation of stock sizes and fishery-effects on mussel population dynamic. - Submitted til Fisheries Research.

1. Indledning

Blåmuslingen, *Mytilus edulis* L., er en vigtig komponent i kystnære økosystemer, og udgør et vigtigt led i stoftransporten fra den pelagiske fødekæde til det bentiske system. I eutrofierede områder med høj primærproduktion udgør filtrerende muslinger, under gunstige opblandingsforhold af vandsøjlen, et vigtigt kontrollerende element af fytoplankton biomassen (Cloern 1982, 1991, Officer *et al.* 1982, Loo og Rosenberg 1989, Møhlenberg 1995). Der er således en miljøforvaltnings-interesse i at opretholde en tæt bestand af bentiske filtratorer i kystnære områder.

Blåmuslinger etablerer sig i banker, hvis fysiske tilstedeværelse påvirker det omgivende økosystem betydeligt. Bankerne øger bundens ruhed og fremmer dermed bundfældelsen af organiske og uorganiske partikler. Dette, sammen med muslingernes afgivelse af fæces og pseudofæces, øger den underliggende havbunds organiske indhold. Samspeilet mellem muslingebankernes komplekse struktur og det øgede fødegrundlag fra tilført organisk materiale muliggør etableringen af en beriget associeret fauna (Seed og Suchanek 1992, Tsuchiya og Nishihira 1985, 1986).

Der er i danske farvande et omfattende fiskeri på naturlige blåmuslingebestande. Undersøgelser i Limfjorden har estimeret bestanden af blåmuslinger til at udgøre ca. 600.000 tons (vådvægt) i 1993-1995. Den årlige fangst er på over 100.000 tons, eller ca. 15% af bestanden årligt. I de enkelte fiskeriområder (se fig. 1) kan landingerne dog udgøre mere end 38 % af bestanden. Muslingefiskeriet er således en væsentlig strukturerende faktor af Limfjordens muslingebestande (VI).

En forudsætning for en biologisk bæredygtig udnyttelse af nationale fiske- og skaldyrsbestande er et fundamentalt kendskab til deres populationsdynamik og deres rolle i det omgivende økosystem. Således er formålet med de undersøgelser, der præsenteres her, at beskrive strukturen i muslingebanker. Undersøgelserne fokuserer på den strukturelle betydningen af muslingernes fasthæftelse til andre muslinger og muslingernes morfologiske variation i banken. Blåmuslingernes dannelse af banker påvirker muslingernes fødeoptagelse og vækst, ligesom den også påvirker interaktionerne med andre marine arter. Effekten af bankedannelsen i relation til disse aspekter er ligeledes undersøgt.

I det følgende vil jeg kort præsentere de artikler, der indgår i sammenfatningen

I. Dolmer, P. The structure of *Mytilus edulis* beds: effects of small-scale seston distribution. - Manuskript.

Fordelingen af fytoplankton, organiske og uorganiske partikler og iltindhold blev målt i vertikale profiler på to muslingebanker i Kaas og Løgstør Bredninger i Limfjorden. Profilerne strakte sig fra 2 meter over muslingebanken til 5 cm ned i muslingebanken. Tætheden af fytoplankton aftog ned mod muslingebanken, med den tydeligste gradient i Løgstør Bredning, hvor også den laveste vandbevægelse blev målt. På begge stationer målttes i overfladen af muslingebanken en fytoplankton tæthed på ca. 1000 celler ml⁻¹. De hydrodynamiske bundforhold havde betydning for muslingernes fødeoptagelse. Således målttes i Løgstør Bredning et større klorofyl a indhold i maver fra muslinger fra øvre bankelag i forhold til i muslinger fra nedre lag. En tilsvarende forskel i fødeoptagelsen blev ikke observeret i Kaas Bredning. I muslingebanken i Kaas Bredning havde muslingerne øverst i banken en større skallængde end

muslingerne nederst i banken. Ligeledes var længden af muslingernes indre labial palper mindre i de øverste muslingelag i forhold til nederst i banken. Labial palperne bruges til at sortere føden i fordøjelige og ufordøjelige partikler, og længdeforskellene var sammenfaldende med et større indhold af uorganiske partikler nederst i banken. Der blev ikke fundet forskel i muslingernes skalvægt eller tørvægt. Der blev ikke observeret vertikale morfologiske variationer i Løgstør Bredning, hvor muslingerne i banken er løst sammenhæftet.

II. Dolmer, P. & I. Svane. 1994. Attachment and orientation of *Mytilus edulis* L. in flowing water. - *Ophelia* 40: 63-74.

Muslingernes fasthæftelse som funktion af vandbevægelse blev undersøgt i et flume eksperiment. Udover muslingernes fasthæftelse blev også antallet af satte byssustråde og deres fasthæftelse målt. Den potentielle fasthæftelse estimeredes som antallet af satte tråde multipliceret med enkelt trådes gennemsnits-fasthæftelse. Muslingerne øgede deres fasthæftelse og antal af etablerede byssus tråde i strømmende vand (19.4 cm sek^{-1}) i forhold til stillestående vand og i moderat strømmende vand (7.7 cm sek^{-1}). Den målte fasthæftelse udgjorde i både stillestående vand og ved en vandstrøm på 19.4 cm sek^{-1} 47 % af den potentielle fasthæftelse. Muslingerne orienteredes passivt med ventralsiden opstrøms. Målinger af den kritiske hastighed, hvorved en musling fjernes af en vandstrøm, viste, at muslingen var udsat for mindst vandmodstand netop ved en orientering med ventral siden eller umbo opstrøms. Muslingeskallens form bevirker, at muslingen udsættes for en lille vandmodstand, når den med byssus tråden som anker orienteres med ventral siden opstrøms.

III. Dolmer, P., M. Karlsson & I. Svane. 1994. A test of rheotaxic behaviour of the blue mussel *Mytilus edulis* L. - *Phuket Mar. Biol. Cent. Spec. Publ.* 13: 177-184.

Mytilus edulis orientering i strømmende vand blev analyseret for at se om muslingerne havde en rheotaxisk adfærd, og dermed reducerede den modstand de påvirkedes med i strømfeltet eller inducerede en passiv filtration. Feltundersøgelser med stereofotografering af muslingebanker kunne ikke påvise nogen orientering i forhold til strømretningen. Felt eksperimenter og flume eksperimenter kunne heller ikke eftervise en rheotaxisk adfærd. Muslingernes "gap-size" blev ligeledes undersøgt som funktion af muslingernes orientering i forhold til stømmens retning og styrke, og en ikke signifikant tendens til en øget gap-size som funktion af øget strømstyrke blev observeret. Det kunne konkluderes, at blåmuslingen ikke orienterer sig i forhold til en strømretning, idet deres mulighed for at orientere sig begrænses af et net af byssus-bindinger, der stabiliserer muslingebanken.

IV. Dolmer, P. Seasonal and spatial variability in growth of *Mytilus edulis* L. in a brackish sound: comparisons of individual mussel growth and growth of size classes. - Accepteret af Fisheries Research.

En undersøgelse af blåmuslingens vækst, målt på individuelt mærkede muslinger holdt i bur og på diskrete størrelsesgrupper af muslinger, viste, at størrelsesgruppernes vækst i sommerperioden var betydelig større end væksten af individuelt mærkede muslinger. I vinterperioden havde de mærkede muslinger en større vækst end størrelsesgrupperne af muslinger. Med en bimodal størrelsesfordeling med store muslinger i toplaget og små muslinger i bundlaget af en muslingebanke, vil både iltvind og fødemangel resultere i, at små muslinger placeret i bundlaget har en øget mortalitet. Ligeledes vil størrelsesspecifik predation fra *Asterias* i vinterperioden kunne reducere størrelsesgrupperes gennemsnitsstørrelse, hvis søstjernerne fjerner de yderste og større muslinger.

V. Dolmer, P. The interactions between bed structure of *Mytilus edulis* L. and the predator *Asterias rubens* L. - Accepteret af J. Exp. Mar. Biol. Ecol.

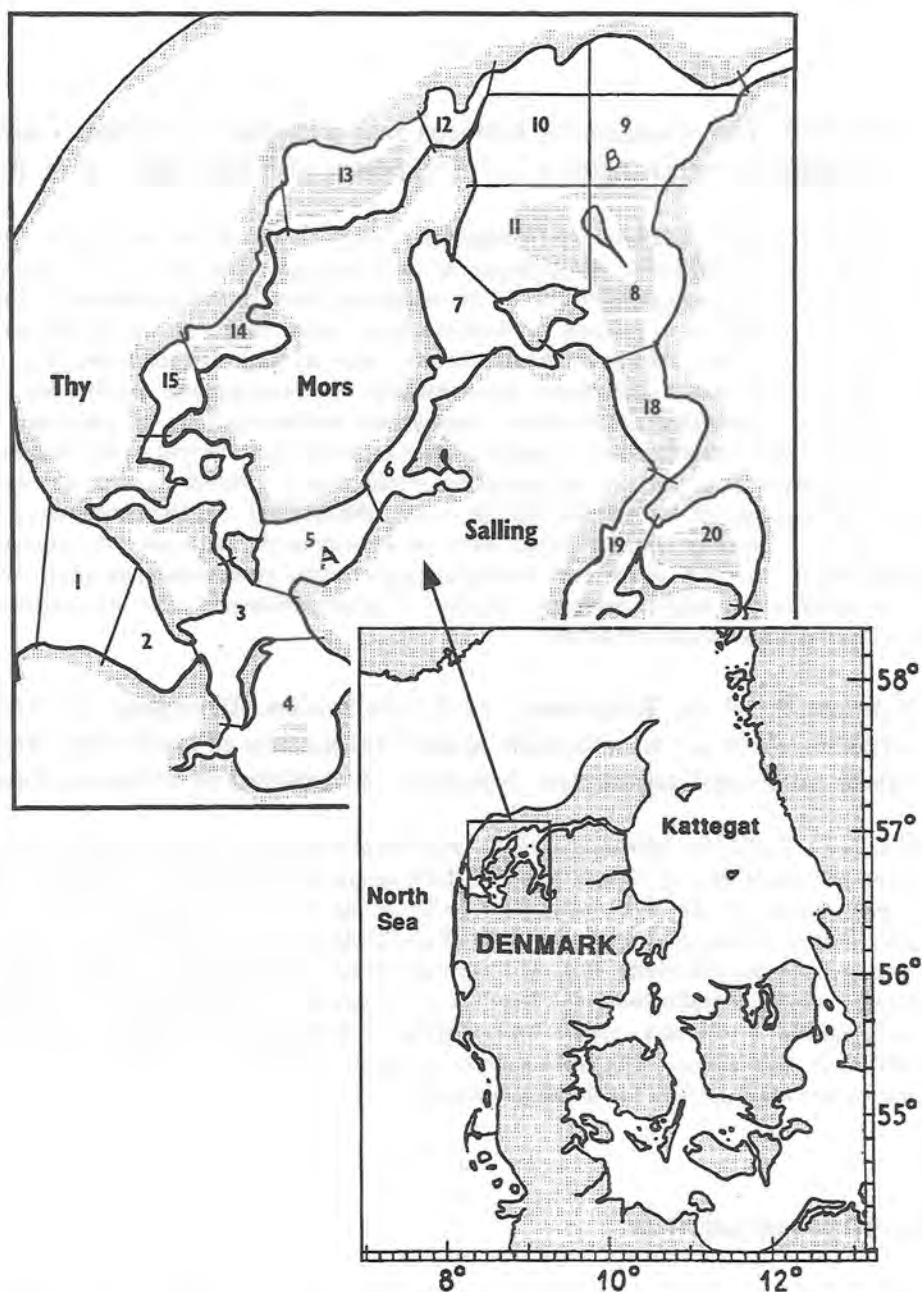
Målinger af blåmuslingernes fasthæftelse på 4 stationer i Limfjorden på 6-8 meters dybde viste en øgning i fasthæftelsen fra 115 til 900 gram, når tætheden af søstjerner blev øget fra 0 til 2.5 individer m^{-2} . Et felteksperiment på en naturlig muslingebanke og akvarieforsøg viste ligeledes en øgning i fasthæftelsen i bure/akvarier med søstjerner i forhold til bure/akvarier uden søstjerner. I felteksperimentet var predationsraten højere i bure med intakt bankestruktur, hvor muslingerne sad bedre fast, i forhold til bure, hvor strukturen var opløst. Tilsvarende akvarieforsøg, hvor muslingerne etableredes i 24 timer og herefter blev frigjort i halvdelen af akvarierne umiddelbart inden tilsætning af søstjerner, viste ingen forskel i predationsraten. Muslingernes orientering med posterior siden op fra banke overfladen, øgede søstjernernes mulighed for at placere sig rigtigt på muslingerne i forbindelse med åbningen af disse. Orienteringen af muslingerne var således vigtigere end fasthæftelsen. Feltindsamlinger af søstjerner i færd med predere en musling viste, at søstjernerne på enkelte stationer prederede muslinger med en gennemsnitsstørrelse, der var større end muslingepopulationens gennemsnitsstørrelse, hvorimod det modsatte var tilfældet på andre stationer. Hverken i felteksperimentet eller akvarieforsøget havde søstjernerne en størrelsesspecifik predation.

VI. Dolmer, P.; P. S. Kristensen og E. Hoffmann. Dredging of blue mussels (*Mytilus edulis* L.) in a Danish sound: estimation of stock sizes and fishery-effects on mussel population dynamic. - Submitted til Fisheries Research.

Blåmuslingen har i Limfjorden stor økologisk og økonomisk betydning. Bestandsstørrelsen blev i 1993-1995 estimeret til mellem 494 og 770.000 tons. Fiskeriet af muslinger udgjorde i perioden årligt 15 % af bestanden, men lokalt blev der målt udnyttelsesgrader på op til 38 %. I perioden 1993-94 påvirkede fiskeriet størrelsen af muslingebestandene, hvorimod en tilsvarende effekt ikke kunne ses i 1994-95, hvor iltsvind i sommerperioden påvirkede 30 % af Limfjorden areal. I områder med iltsvind observeredes en 33 % nedgang i muslinge bestandene, hvorimod en 46 % øgning i bestandsstørrelserne registreredes i områder uden iltsvind. Limfjorden opfylder mange af de kriterier, der er opstillet for et område, hvor de bentiske filtratorer kontrollerer fytoplankton-populationerne. Fjernelsen af filtrerende muslinger kan således have en stor effekt på hele Limfjordens økosystem.

2. Undersøgelsesområde

Limfjorden, der har dannet ramme for undersøgelserne præsenteret i (I, IV, V og VI), er et 1575 km^2 stort sund, der forbinder Nordsøen i vest med Kattegat i øst. Tidevandsforskellene er meget små i Limfjorden, der er gennemløbet af en vest-øst rettet vandstrøm med en gennemsnitlig vandopholdstid på 1½ år. Saliniteten varierer fra 32 promille i den vestlige del til 22 promille i den østlige Limfjord. Vandet er meget næringsrigt, idet Limfjorden afvander et opland på 7500 km^2 , der hovedsageligt består af landbrugsland. Vandets indhold af klorofyl i sommerperioden varierede således i perioden 1982-1993 fra 6-7 $\mu g\ l^{-1}$ i de åbne bredninger som Nissum, Løgstør og Thisted Bredninger og op til 20 $\mu g\ l^{-1}$ i de lukkede bredninger som Skive Fjord (Limfjordsovervågningen 1995). De lukkede dele af fjorden som Skive Fjord, Lovns Bredning og den sydlige del af Løgstør Bredninger er med få års mellemrum påvirket af omfattende iltsvind. Iltsvindet opstår efter perioder med stor primærproduktion og ringe opblanding af vandsøjlen.



Figur 1. Kort over Limfjorden med angivelsen af opdelingen i fiskeriområder (1-20). Område der hyppigt er påvirket af iltsvind er markeret. De to stationer i Kaas og Løgstør Bredninger er markeret med henholdsvis et A og B.

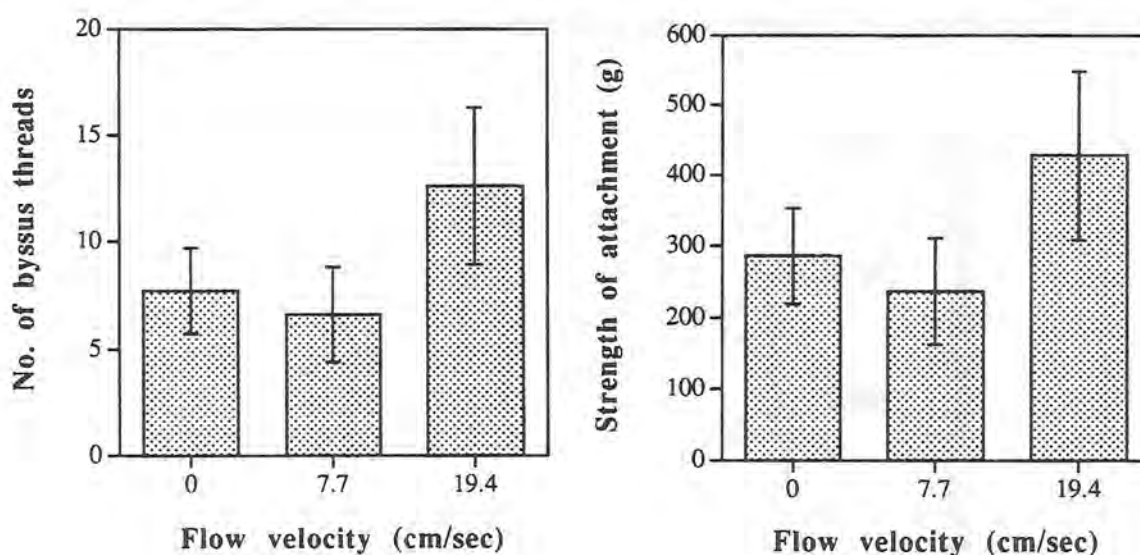
3. Beskrivelse af en muslingebanke

Blåmuslingebanke kan opdeles i tre strukturelle komponenter (Seed og Suchanek 1992). Banker består af fysiske matricer af sammenhæftede muslinger og døde skalfragmenter og et bundlag med stort organisk indhold af sedimenterede partikler, pseudofæces og fæces fra muslingerne. Den tredje komponent består af den associerede flora og fauna, der sammen med blåmuslingerne udgør *Mytilus*-samfundet. Muslingebankernes kompleksitet med øget overfladeareal og dannelsen af mikrohabitater med refugie-muligheder og det organisk berigede sediment understøtter en høj artsdiversitet (Tsuchiya og Nishihira 1985, 1986).

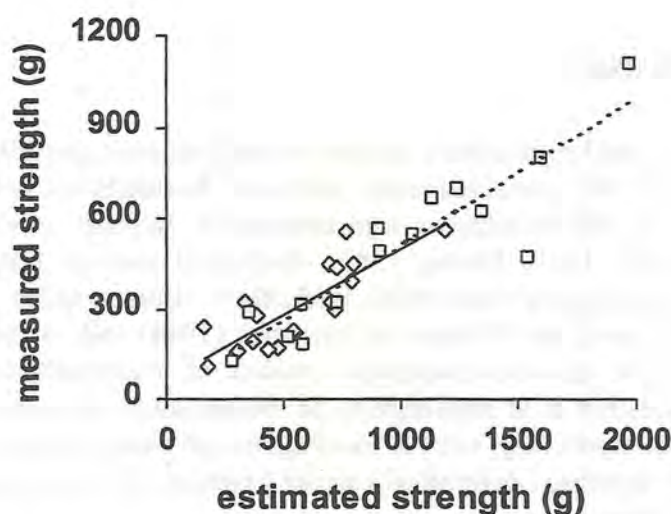
3.1 Byssusfasthæftelse

En vigtig komponent i muslingebankers struktur er muslingernes gensidige fasthæftelse og evt. fasthæftelse til et fast primærsubstrat. Styrken af fasthæftelsen er bestemt dels af muslingens størrelse og dels af faktorer som temperatur, salinitet, lufteksponering og substrattype (van Winkle 1970, Young 1983). Endvidere varierer fasthæftelsen med årstiden, således at muslingen er mest solidt fasthæftet i vinterperioden (Price 1980). I muslingebanker på hårbund har Witman og Suchanek (1984) målt, at muslinger tæt på bankekanten sidder bedre fast end muslinger i midten af muslingebanken. Forskellen kan skyldes en kombination af at muslingerne på bankekanten stimuleres kraftigere til fasthæftelse ved bølgeeksponering, samt at muslingerne på bankekanten i højere grad er fasthæftet til det faste underlag i forhold til centralt i banken, hvor muslingebanken ofte består af flere lag muslinger.

Blåmuslingers fasthæftelse er endvidere påvirket af vandbevægelse (II). I et flume eksperiment målte fasthæftelsen og antallet af satte byssustråde på blåmuslinger, der havde været placeret i stillestående, langsomt eller hurtigt strømmende vand (7.7 eller 19.4 cm sek⁻¹). Muslinger, der var placeret i hurtigt strømmende vand, satte flere tråde og var bedre fasthæftet end muslinger i stillestående eller langsomt strømmende vand (Fig. 2). Fasthæftelsen af enkelte byssustråde blev ligeledes målt, og ved at multiplicere fasthæftelsen af enkelte tråde med antallet af etablerede tråde, kunne en potentiel fasthæftelsesstyrke estimeres. Den målte fasthæftelse udgjorde i eksperimentet 47 % af den potentielle fasthæftelse, og der var ikke forskel i udnyttelsen af den potentielle fasthæftelse af muslinger i stillestående og hurtigt strømmende vand (Fig. 3).



Figur 2. Fasthæftelsen og antal byssushæftninger som funktion af strømstyrke (II).



Figur 3. Sammenhæng mellem estimeret fasthæftelse og målt fasthæftelse af muslinger i stillestående vand (◇) og 19.4 cm s^{-1} (□). Den ubrudte regressionslinie er for stillestående vand, og den stiplede linie er for 19.4 cm s^{-1} (II).

Tilstedeværelsen af søstjernen *Asterias rubens*, der er en vigtig predator af blåmuslinger, påvirker også fasthæftelsen (V). Blåmuslingers fasthæftelse var tydeligt korreleret med tætheden af søstjerner på fire stationer i Limfjorden. Fasthæftelsen varierede fra 115 g på stationen uden søstjerner til 900 g på stationen med 2.5 søstjerner m^{-2} (Fig. 4). For at teste, om det observerede mønster skyldes en stimulering til en øget fasthæftelse hos muslingerne eller opstod som følge af predatorens fjernelse af de mest løstsiddende muslinger, målte i et bureksperiment og akvarieforsøg fasthæftelsen af muslinger eksponeret for søstjerner og kontrol muslinger. I både felt- og laboratoriet blev der målt en øget fasthæftelse, når muslingerne var i kontakt med søstjerner.

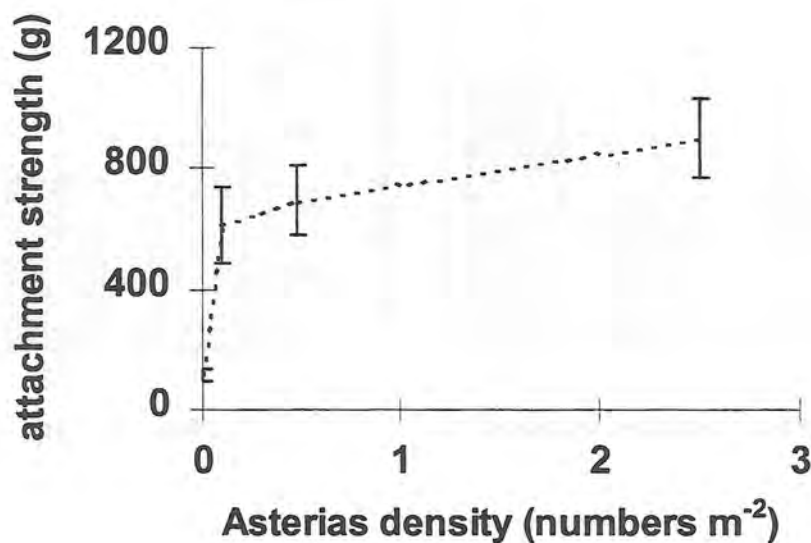


Fig. 4. Blåmuslingers fasthæftelsesstyrke på 4 stationer i Sallingsund og Løgstør Bredning som funktion af tætheden af søstjerner (V).

3.2 Blåmuslingers morfologiske variation i muslingebanker

Som tidligere omtalt danner blåmuslinger komplekse banker af sammenbundne muslinger, der optager føde og ilt fra de omgivende vandmasser. Både fødepartiklerne og ilten antager tredimensionelle mønstre over bankerne, hvorover der er observeret lavere koncentrationer af fytoplankton og andre partikler (Fréchette og Bourget 1986a, Asmus og Asmus 1991, I). Ligeledes er der målt horisontale variationer i iltkoncentrationerne, med laveste koncentrationer centralt over muslingebanker i forhold til i bankernes periferi (Jørgensen, 1980). Disse fordelingsmønstre vil i et samspil med de hydrodynamiske forhold over banken resultere i, at muslingerne opbygger en rumlig variation af bestemte morfologiske karakterer. Således har de muslinger, der lever på randen af en muslingebanke en større skallængde end muslingerne centralt i muslingebanken (Newell 1990, Svane og Ompi 1993). Også i et vertikalt plan er der målt størrelsesforskelle i mytilider (Kautsky 1982, Alvarado and Castilla 1996). Kautsky (1982) målte således i den svenske Østersø skærgård et højere antal af små blåmuslinger nederst i en muslingebanke. De små muslinger er underlagt de større muslinger i toplaget i konkurrencen om føde, og først efter fjernelse af de større muslinger vokser de små muslinger og overtager således de store muslingers plads.

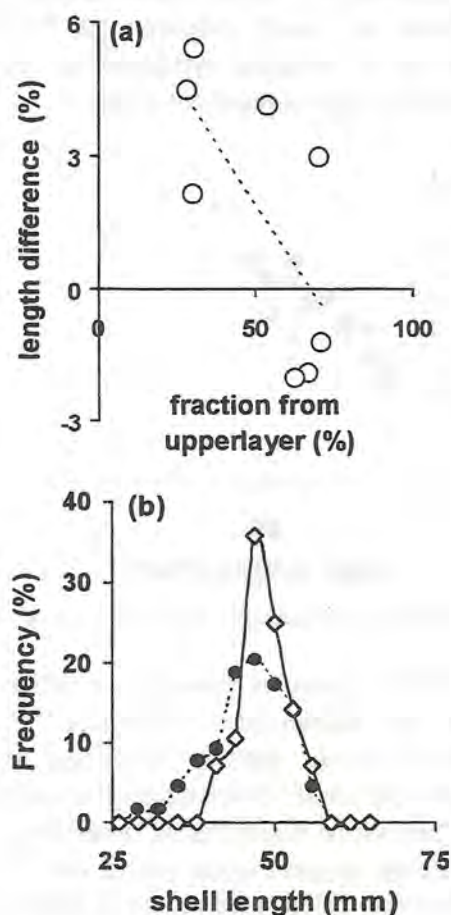
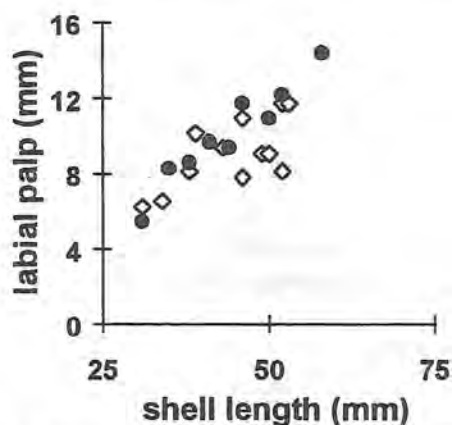


Fig. 5. Lagdeling i gennemsnitsstørrelsen mellem øvre og nedre lag i en muslingebanke i Kaas Bredning. a) Den relative forskel i skallængde mellem muslinger i øvre og nedre lag som funktion af separationsdybde, målt som fraktion af muslingerne i delprøve fra øvre lag. b) Længde fordeling af muslinger fra øvre lag (\diamond) og nedre lag (\bullet) (I).

I Limfjorden er der også målt vertikale forskelle i gennemsnitsstørrelserne af blåmuslinger (I). På muslingebanker i Kaas og Løgstør Bredninger, blev der indsamlet muslinger ned gennem muslingebanken fra henholdsvis øverste og nederste bankelag. Muslingerne blev indsamlet med en ramme (25 x 25 cm), som blev presset ned i banken, hvorefter en kniv kunne skydes ind i et horisontalt plan og separere muslingebanken i en øvre og nedre del. I Kaas Bredning observeredes en korrelation mellem andelen af muslinger i prøven fra øvre lag og størrelsesforskellen mellem øverste og nederste lag (Fig. 5a). Når andelen af muslinger i øverste prøve var lille, d.v.s. at banken var separeret tæt under overflade, var forskellen mellem længden af de øverste og nederste muslinger størst. En varians-analyse af de prøver, hvor andelen af muslinger i den øverste del udgjorde 30%, viste en signifikant størrelsesforskel. Hvis vi betragter længdefordelingerne af muslinger indsamlet fra øverste og nederste bankelag ses, at muslingerne fra begge lag udgør en enkelt størrelsesgruppe. Endvidere er frekvensen af de større muslinger ens for de to delprøver, hvorimod frekvensen af mindre muslinger er størst i de nederste lag (Fig. 5b).

Muslingerne filtrerer en suspension af fordøjelige og ufordøjelige partikler. Når partikeltætheden kommer over 1 mg l^{-1} (Kiørboe *et al.* 1981) har muslingerne brug for at kunne sortere frafiltrerede partikler. Andre undersøgelser af Kiørboe og Møhlenberg (1981) har vist, at størrelsen af labial palperne på forskellige muslingearter var korreleret med artens evne til at adskille fytoplankton fra silt. Men den egentlige sorterings-mekanisme er ikke klarlagt (Jørgensen 1990).



Figur. 6 Længden af indre labial palper fra muslinger i øvre lag (◇) og nedre lag (●) (I).

Undersøgelser af Theisen (1982) viste, at størrelsen af blåmuslingers labial palper var korreleret med mængden af suspenderet materiale i deres omgivende miljø. Blåmuslingerne i Vadehavet havde således betydelig længere labial palper end muslingerne i de indre danske farvande. Blåmuslingerne i Kaas Bredning viste også stor morfologisk variation med hensyn til størrelsen af deres labial palper (I). Således havde muslingerne i de nedre bankelag længere labial palper end muslingerne øverst i banken. Muslingerne nederst i banken kan således forventes at udføre et større sorteringsarbejde i forbindelse med optagelse af føde. Ved målinger af partikeltætheden i en profil over muslingebanken blev der observeret en højere tæthed af ikke fluorescente partikler nær bunden, hvilket gør det fordelagtigt for muslingerne, at have store labial palper. Ligeledes vil pseudofæces og fækale partikler fra øverst i banken bundfælde i de nedre

bankelag, hvilket også vil øge behovet for et effektivt sorteringsorgan hos muslingerne nederst i muslingebankerne.

I muslingebanken i Løgstør Bredning blev der ikke observeret en tilsvarende forskel mellem øvre og nedre lag af muslingebanken. Fasthæftnings-mønstrene mellem muslingerne i bankerne var ligeledes meget forskellige (V). Den meget faste bankestruktur i Kaas Bredning, med begrænsede muligheder for muslingerne for at ændre position eller orientering, muliggør en udvikling af vertikale variationer i morfologiske karakterer.

3.3 Muslingernes orientering

Adskillige rækker af marine invertebrater orienterer sig i forhold til strømmens retning. Denne adfærd kaldes rheotaxi. Mange af de arter, der har en rheotaxisk adfærd, inducerer en passiv filtration, som resultat af deres rheotaxi. Gode eksempler på passiv filtration finder vi hos svampe (Vogel 1974), gorgonier (Wainwright og Dillon 1969), kammuslinger (Hartnoll 1967), sabellide børsteorm (Merz 1984), slangestjerner (Rosenberg 1995), og ascidier (Young og Braithwaite 1980). Hos muslingerne ses eksempler på en orienteringsadfærd, der reducerer opblandingen af exhalent og inhalent vand. Muslingerne *Geukensia* og *Mya* orienterer sig begge med siphonerne på tværs af strømretningen (Frey *et al.* 1987, van Vincent *et al.* 1988) og reducerer dermed opblandingen af fødefattigt exhalent vand og føderigt inhalent vand. Da muslingerne ofte orienterer sig med posterior siden opad, og deres exhalente siphon-åbning er større end den inhalente åbning, vil vand-jets fra exhalente siphoner kunne inducere en opblanding af de nedre bundnære vandlag, og dermed øge transporten af fødepartikler ned til de filtrerende muslinger. (O'Riordan *et al.* 1995).

Orienteringen hos blåmuslinger er undersøgt i Strömmarna på Sveriges vestkyst (III). Undersøgelserne testede om blåmuslingerne ved at orienterer den inhalente siphon op mod strømmen og den exhalente væk fra strømmen, således at der opstod en trykforskel, kunne etablere en passiv filtration. Muslingernes orientering blev målt i en 300 meter lang kanal, hvor strømhastigheder op til 100 cm sek⁻¹ er målt. Muslingernes orientering blev registreret på billeder taget med stereokamera. Analysen af billederne viste ingen foretrukne orienteringer. I et felteksperiment blev der på lokaliteten udsat seks kasser fyldt med sediment og med plantede muslinger orienteret i forskellige retninger i forhold til strømretningen. Kasserne gravedes ned i bunden for at undgå at påvirke strømforholdene. Kasserne blev stereofotograferet lige efter udsætningen og de følgende to dage. Efter én dag havde muslingerne ikke ændret deres orientering, hvorimod muslingerne efter 2 dage havde en tilfældig orientering, der var uafhængig af start orienteringen. Der var således ikke en enkelt fordelagtig orientering, der blev bibeholdt (Fig. 7).

Wildish og Saulnier (1992) målte væksten af kammuslinger og observerede en lavere vækst ved høje strømhastigheder. På baggrund af muslingernes fysiologi og indretning af filtrations-apparatet afviste Jørgensen (1990), at passiv filtration kan spille en rolle for muslingernes fødeoptagelse. Et forhøjet vandtryk på den inhalente side af gællefilamenterne vil sammentrykke disse og dermed øge vandmodstanden i systemet gennem muslingen.

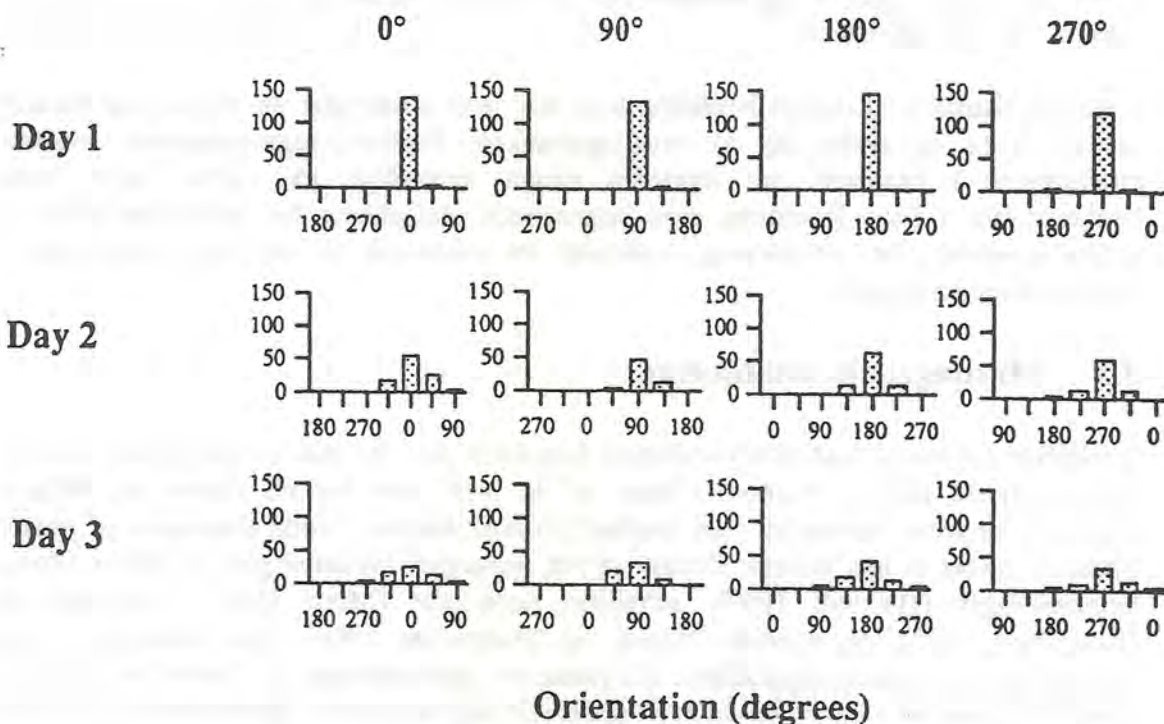


Fig. 7. Fordelingen af orienteringsretninger i felteksperiment med blåmuslinger ved start, og efter 24 og 48 timer efter udsætningen. Muslingerne var på starttidspunktet etableret i blokke med deres sagittale plan orienteret henholdsvis 0, 90, 180 eller 270 grader i forholdt til strømretningen (III).

Muslingernes skal-morfologi og orientering bestemmer den kraft som modstanden fra strømmende vand påvirker dem med. Muslingernes specielle vingeform kan således antages at være en tilpasning til livet i strømmende vand. Flume-undersøgelser viste, at den modstand, som muslingerne ydede, var afhængig af deres orientering (II). Således var modstanden lavest når muslingerne orienteredes med umbo eller ventral siden op mod strømmen. På et glat underlag orienteredes muslingerne netop med ventral siden opstrøms, idet byssus fasthæftelsen virkede som et anker, der dermed drev muslingen over i denne position.

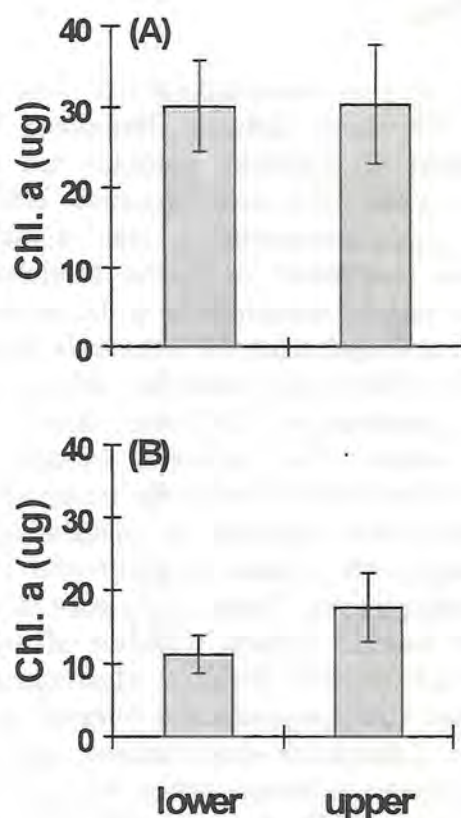
Som tidligere nævnt udgør muslingernes intraspecifikke fasthæftelse en afgørende rolle for, om muslingerne kan udvikle strukturmønstre i muslingebanker. Fasthæftelsen vil virke begrænsende for muslingernes mulighed for at udføre en rheotaxisk adfærd. Netop eftervisningen af morfologisk lagdeling i muslingebanker (Kautsky 1982, Alvarado og Castilla 1996, I) viser, at strukturen i muslingebanker er fastlåste, med små muligheder for muslingerne til ændringer i orientering eller position.

4 Fødebegrænsning

Laboratorie-undersøgelser har vist, at store blåmuslinger har en filtrationskapacitet på op til 80 liter vand i døgnet. I lavvandede kystområder, med store muslingebestande, vil muslingernes filtrationspotentiale svare til, at hele vandsøjlen filtreres flere gange

dagligt. Idet den bentiske filtration både er begrænset af mængden af suspenderede fødepartikler, men også af opblandingen og transporten af fødepartiklerne ned til bunden, vil den effektive filtration ofte være meget lavere end den potentielle filtration. Adskillige undersøgelser har således dokumenteret, at tætte bestande af bentiske filtratorer er istand til at fortynde partikeltætheden over bankerne og at opbygge et partikel-grænselag (Frechette og Bourget 1986a, Asmus og Asmus 1991, Butman *et al.* 1994) og dermed begrænse deres vækst (Frechette og Bourget 1986b, Petersen *et al.* 1997). Møhlenberg (1995) observerede en faldende koncentration af klorofyl mod bunden over en muslingebanke i Roskilde Fjord, når opblandingen af vandsøjlen var lille. Derimod var klorofyllet jævnt fordelt over vandsøjlen ved høje opblandingsrater, hvor en reduktion i klorofyl koncentrationen som funktion af tid kunne ses. Denne reduktion skyldes de bentiske filtratores øgede græsning ved en øget opblandingsrate. Man kan således tale om, at de bentiske filtratorer bliver afkoblet fra det pelagiske system, når vandsøjlen ikke opblandes.

Opblandingen har også betydning for transporten af fødepartikler ned i selve muslingebanken. Undersøgelser i Kaas og Løgstør Bredninger (I) viste, at muslingerne nederst i en muslingebanke havde en reduceret fødeoptagelse i forhold til muslingerne i bankeoverfladen, når vandbevægelsen over muslingebanken var svag (2.6 cm sek^{-1}). Derimod var der ingen vertikal variation i fødeoptagelsen ved en kraftigere strømstyrke (4.5 cm sek^{-1}) (Fig 8).



Figur 8. Klorofyl a indholdet i blåmuslinger indsamlet i øvre og nedre lag i muslingebanker i Kaas Bredning (A) og Løgstør Bredning (B) (I).

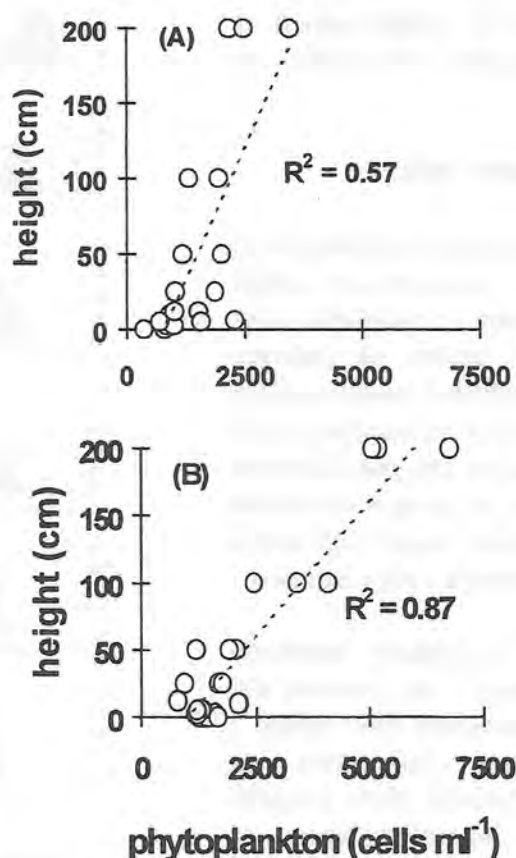
De observerede forskelle i fødeoptagelsen hos muslinger, som funktion af deres placering i muslingebanken, kan skyldes fødekongurrence mellem muslingerne om de partikler, der transporteres ned i banken, men kan også skyldes pladskongurrence (Fréchette *et al.* 1992). For koloniale dyr som blåmuslinger, hvor plads og fødeforhold er så integrerede i hinanden, har de to konkurrence-parametre (føde/plads) tidligere været betragtet som værende afhængige af hinanden. Fréchette *et al.* (1992) gennemførte et eksperiment, hvor føde- og pladskongurrence kunne adskilles. En ens mængde muslinger blev holdt i forskellige tætheder i fire linier af gennemstrøms-akvarier, men med samme tilførsel af føde. De muslinger, som blev holdt i få høje tætheder, og altså var pladsbegrænsede, havde en langsommere vækst. Fréchette *et al.* (1992) postulerede, at pladskongurrence kunne opstå, når muslingernes mulighed for at åbne skallerne begrænsedes, og dermed reducerede fødeoptagelsen. Den reducerede fødeoptagelse nederst i banken i Løgstør Bredning kan således både være et resultat af fødekongurrence, men kan også skyldes pladskongurrence. Strukturen i muslingebanken i Løgstør Bredning var betydeligt løsere end i banken i Kaas Bredning (V). Hvis fødeoptagelsen hos muslingerne var pladsbegrænset ville en reduceret fødeoptagelse først kunne forventes i en bank med fast struktur, altså i Kaas Bredning. En begrænset fødeoptagelse i en bank med løs struktur er altså en indikation af, at konkurrencen om føde har større betydning end konkurrencen om plads.

4.1 Fødepartiklers fordeling

Fordelingen af fødepartikler over og i en muslingebank er, som beskrevet i forrige afsnit, påvirket af de bentiske filtratorers aktivitet. Derudover er der forskellige transportmekanismer, hvis transport af organiske partikler ned til filtratorerne er essentiel for deres fødeoptagelse. Vind- eller strøm induceret diffusiv transport er i lavvandede marine områder en vigtig transportform, idet vandsøjlen her vil være fuldstændig opblandet når vinden overskrider en kritisk hastighed, der er positivt korreleret med vanddybden. Den anden transportform er horisontal advektion, hvor strømmen fører partikler ind over muslingebanken fra tilstødende områder. Betydningen af denne transportform er lille i et område som Limfjorden. Dels er strømhastighederne ofte små ($<5 \text{ cm sek}^{-1}$), og dels er muslingerne i Limfjorden struktureret i en mosaik af banker af varierende størrelser, således at en horisontal transport blot vil flytte et vandvolumen fra den ene bank til den næste. Den tredje transportform er biomixing, hvor muslingernes egen pumpeaktivitet medfører en opblanding af de bundnære vandlag. Butman *et al.* 1994 analyserede i flume eksperimenter ($5 \text{ og } 15 \text{ cm sek}^{-1}$) planktonfortyndingen over en muslingebank. Deres steady state model (se Fréchette *et al.* 1989) var opbygget som en balance mellem transport af alger ved horisontal advektion og vertikal mixing og muslingernes filtration. Muslingernes egen biomixing var ikke inddraget, idet de exhalente flowhastigheder ved filtration var meget lavere end *boundary shear* hastigheden (u_*). Laboratorie-eksperimenter med muslinge-atrappes har vist, at vandstrømmen fra muslingers exhalente siphon bidrager til en opblanding af de nederste vandlag (O'Riordan *et al.* 1995); et resultat som også Larsen og Riisgård (1997) viste hos ascidier i akvarieeksperimenter med stillestående vand. Effekten af turbulent mixing fra de overliggende vandlag og ned i banken dæmpes af strukturerne i muslingebanken. Denne dæmpning vil øge betydningen af biomixing, som energikilde til partikel transport internt i banken. Det lavere indhold af klorofyl, der

blev målt i muslingemaver nederst i banken i Løgstør Bredning (I) viser, at biomixing ikke kan udligne forskellene i fødekonzentrationer i banken og erstatte manglende transport fra de to andre transportmekanismer i banken. Ved lave opblandingsrater kan biomixing således ikke kompensere for faldet i partikeltransport som advektion eller turbulent mixing internt i banken.

Ser man på fordelingen af fytoplankton over muslingebankerne (I) ses i Kaas Bredning et fald fra 2650 celler l^{-1} målt 200 cm over bunden til 767 celler l^{-1} målt i overfladen af muslingebanken. De tilsvarende tætheder i Løgstør Bredning var 5665 og 982 celler l^{-1} (Fig. 9). Det største fald i fytoplankton koncentrationen blev således målt i Løgstør Bredning, hvor også den laveste strømhastighed blev målt. Møhlenberg (1995) fandt et tilsvarende forhold i Roskilde Fjord, hvor han målte en reduceret klorofyl koncentration tæt ved bunden under lave opblandingsrater, hvorimod en homogen fordeling af klorofyl over hele vandsøjlen blev målt efter en periode med vind induceret opblanding. Også fytoplanktonets evne til at placere sig i vandsøjlen med positiv eller negativ fototaxi vil påvirke deres fordelingsmønstre (Valiela 1984), men forskellene i muslingernes klorofyl indhold viser, at opblandings-raten kombineret med muslingernes filtration udgør en vigtig kontrollerende komponent af fytoplanktonnet.



Figur 9. Vertikale profiler af fytoplankton koncentrationen i Kaas Bredning (A) og Løgstør Bredning (B) (I).

Tætheden af fytoplankton i overfladen af muslingebankerne i Kaas og Løgstør Bredninger var henholdsvis 767 og 982 celler l^{-1} (I). Riisgård og Randsløv (1981) målte i et laboratorieeksperiment, at muslingerne reducerede deres filtrations rate, når tætheden af fytoplankton var mindre end 1500 celler l^{-1} . Omregning af data fra et flumeeksperiment (Butman *et al.* 1994) viste, at muslingerne ikke udviklede et koncentrations grænselag af fytoplankton, når fytoplankton tætheden var under 1040 celler l^{-1} (I). Muslingerne i naturlige muslingebanker vil således kun filtrere ned til en fytoplankton tæthed på omkring 1000 celler l^{-1} , hvorefter filtrationsraten reduceres.

5 Blåmuslingers vækst

Den energi, som blåmuslingerne optager via deres filtration, forbruges i muslingernes metaboliske processer og til vækst, herunder produktion af kønsprodukter. Væksten er afhængig af en række faktorer som temperatur, alder, salinitet og genotype (Kautsky *et al.* 1990, Seed og Suchanek 1992), kvantitet og sammensætning af seston (Kiørboe *et al.* 1981, Small og van Stralen 1990) og opblandningsraten af bundnære vandlag over muslingerne (Frechette og Bourget 1985b).

5.1 Individ - og populations-vækst

Væksten af blåmuslinger kan bestemmes ved brug af to fundamentalt forskellige metoder. Væksten kan måles på individuelle muslinger, der enten er mærkede eller holdt i bur, eller væksten kan måles på diskrete størrelsesklasser af muslinger. Forskelle i vækst mellem enkelte muslinger og størrelsesklasser af muslinger kan tilskrives størrelsesspecifik mortalitet hos populationen (Seed og Suchanek 1992). Således vil en øget mortalitet af mindre muslinger i en population kunne registreres ved en øgning af gennemsnitsstørrelsen i populationen.

I Limfjorden blev væksten af individuelt mærkede muslinger undersøgt på 16 stationer i den centrale del af Limfjorden i 1995 (IV). Muslingerne blev udlagt i bure i perioderne januar-marts, juli-august og november-december. I samme periode blev længdeudviklingen målt på diskrete størrelsesklasser af muslinger på 4 stationer (Fig. 10). Fra januar til marts målt en lille gennemsnits-tilvækst af de mærkede muslinger på 0.12 mm. Størrelsesklasserne, derimod, havde en reduktion på 0.45-3.5 mm i perioden januar-april. I sommerperioden fra juli til august blev der målt

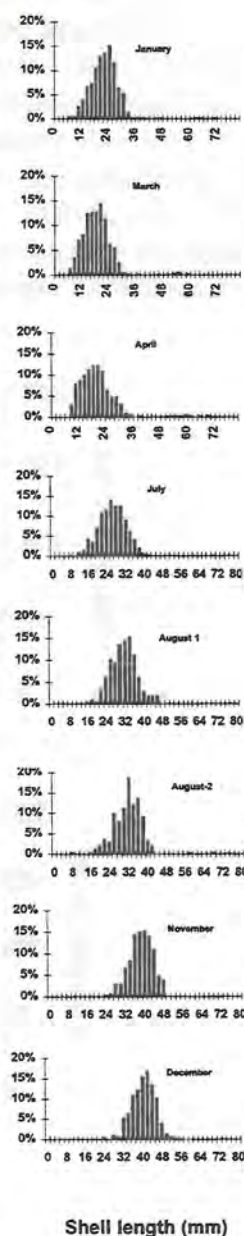


Fig. 10 . Størrelsesfordelingen af *Mytilus edulis* som funktion af tid i Løgstør Bredning (IV).

en individuel tilvækst mellem 0.13-1.98 mm, hvorimod størrelsesklasserne øgede deres skallængde med 5.4 til 6.3 mm. I november-december blev der ikke observeret forskelle i vækstmønstrene af henholdsvis individuelle og størrelsesklasser af muslinger. De modsatrettede forskelle mellem individuel og størrelsesklasse vækst i vinter og sommer perioderne indikerer, at størrelsesspecifik mortalitet er en væsentlig faktor for størrelses sammensætningen i muslingebankerne i Limfjorden.

5.2 Rumlige vækstofforskelle

En analyse af den rumlige variation i væksten, målt på 16 stationer, viste ingen forskelle i væksthastigheden i perioden januar-marts. I juli-august var væksten størst i den vestlige del af Limfjorden og på en enkelt station i Løgstør Bredning. I november-december blev muslingerne i de vestlige bredninger ikke inddraget i en analyse p.g.a. indtrængning af søstjerner i burene. Ved at sammenligne størrelsesfordelingen af diskrete størrelsesklasser af muslinger på 126 stationer i maj 1993 og 1994 kunne væksten i de forskellige områder i Limfjorden sammenlignes. Væksten blev beskrevet med von Bertalanffy's vækst ligning: $l_t = l_{\infty} - (l_{\infty} - l_0)e^{-Kt}$ hvor l_0 og l_{∞} er henholdsvis konstanter for muslingens længde til tiden 0 og maksimum længde, t er tid og K er vækstraten. Blåmuslingernes vækst i Limfjorden er hurtig, sammenholdt med målinger fra andre danske og nordeuropæiske kystområder (Tabel 1).

Location	l_{∞}	K	Author
Limfjord, DK	52.8-69.0	0.31-1.42	present study
Mariager Fjord, DK	80.8-86.3	0.35-0.45	Theisen, 1975
Gønner Fjord, DK	80.2-108.2	0.14-0.26	---
Randers Fjord, DK	50.7-54.5	0.24-0.31	---
Kolding Fjord, DK	77.2-88.7	0.17-0.16	---
Wadden Sea	77.6	0.56	Theisen, 1968
Plymouth, UK	81.3-93.8	0.22-0.24	Bayne and Worrall, 1980
Askö, Baltic Sea	32	0.12	Kautsky, 1982
Disko, Greenland	77.5-283.9	0.022-0.162	Theisen, 1973
Thule Greenland	94.5-153.3	0.048-0.053	---

Tabel 1. Maksimum skallængde l_{∞} og vækst parameteren K beregnet for blåmuslinger (IV).

Den største vækst, målt på både individuelt og populationsniveau, blev målt i den vestligste del af Limfjorden i Kaas og Venø Bredninger (område 3-5). Området har en for Limfjorden høj salinitet (30-32 ppm), der vil stimulere en hurtig vækst (Kautsky *et al.* 1990). Væksten i Venø Bugt (område 4), umiddelbart syd for området 3-5, er betydeligt langsommere, hvilket indikerer, at de relativt høje saliniteter i område 3-5 ikke forklarer de høje vækstrater. Venø og Kaas Bredninger danner et stræde mellem Nissum Bredning og Limfjordens centrale bredninger, og en vest-øst rettet strøm vil opnå de højeste strømhastigheder/opblandingsrater i dette område. Dette vil øge transporten af fødepartikler ned til de bentiske filtratorer og øge fødeoptagelsen (I). De rumlige variationer i væksten i Limfjorden er ikke korreleret med mængden af føde, målt som klorofyl *a*. I sommerhalvåret er de højeste klorofyl koncentrationer, som

tidligere angivet, målt i de sydlige bredninger (20 mg l^{-1}), hvorimod koncentrationen er betydeligt lavere i område 3-5 (Limfjordsamterne 1995). Væksten er således styret af opblandings-raten af de nedre vandlag, og selv i områder med lave fødemængder, men med høje opblandingsrater, er der føde nok til en hurtig vækst i sommerperioden.

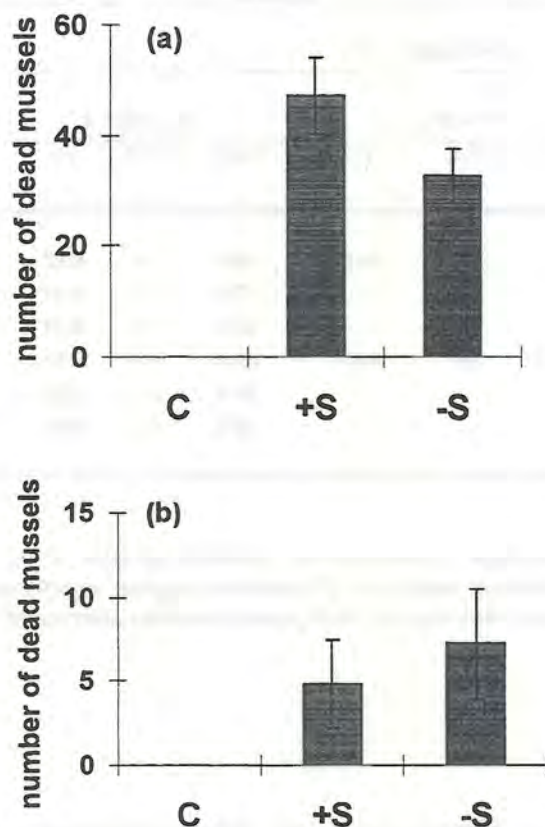
6 Bankestrukturens betydning for predation

I de indre danske farvande er blåmuslinger en vigtig fødekilde for marine invertebrater som strandkrabbe, *Carsinus maenas*, og søstjerne, *Asterias rubens*, og havfugle som strandskade, *Haematopus ostralegus*, og edderfugl, *Somateria molissima*. Både strandkrabben og edderfuglen frigør muslinger fra muslingebanker i forbindelse med deres predation, og bruger således energi på overrivning af byssushæftninger (Ameyaw-Akumfi og Hughes 1987, Rafaelli *et al.* 1990). Undersøgelser af den californiske havodders predation på muslingen *Mytilus californianus* viste, at odderen gentagne gange dykker og indsamler muslinger fra det samme sted, og dermed bryder strukturen og danner en åbning i banken (van Blaricom 1988). Gentagne indsamling af muslinger fra samme sted mindsker dermed den energi, som havodderen efterfølgende skal bruge på at frigøre muslinger fra banken.

Også andre arter udviser en aggregeret adfærd i forbindelse med deres predation af blåmuslinger. Aggregering af søstjerner er et fænomen, der er i beskrevet i sommerperioden fra flere kystlokaliteter (Spärck 1932, Rasmussen 1973, Sloan og Aldridge 1981, Dare 1982). Dare (1982) beskriver, hvordan der dannes tætte aggregater af søstjernen ($300\text{--}400$ individer m^{-2}), der i bånd vandrer hen over en muslingebanke og efterlader den totalt defauneret. Vandringshastigheden er bestemt til 300 meter over en to måneders periode. Aggregeringen er således associeret til områder med høj fødetæthed. Endvidere er den sat i forbindelse med søstjernernes reproduktion, men dens betydning er ikke endeligt klarlagt (Sloan 1980).

Et bureksperiment i Løgstør Bredning viste, at søstjerners predationsrate af muslinger var størst i bure med intakt bankestruktur, hvorimod predationen var mindre, når bankens struktur var ødelagt og alle byssushæftninger brudt (Fig 11a) (V). I tilsvarende akvarieeksperimenter, hvor muslingerne etablerede sig i løbet af 24 timer inden søstjernerne blev placeret i akvarierne, sås ingen forskel i predationsraten af muslinger i den etablerede struktur af muslinger og hvor strukturen igen blev brudt umiddelbart før søstjernerne kom i akvariet (Fig. 11b). De "intakte" muslingebanker i felt- og laboratorie-eksperimenterne adskilte sig tydeligt i deres struktur. I felt-eksperimentet blev predationen målt på en naturlig banke, hvor størstedelen af muslingerne var orienterede med posterior siden opad, hvorimod muslingerne i akvarie-eksperimenterne ikke havde etableret denne struktur efter 24 timer. Christensen (1957) har beskrevet, at søstjerner foretrækker at predere muslinger, der netop er orienteret med posterior-siden opad, idet en åbning af muslingen er lettest, når den kan angribes fra denne vinkel. Ud fra undersøgelserne kan det konkluderes, at predationsraten er højest på muslinger organiseret i en struktur med posterior-siden opad, og at selve fasthæftningen ikke påvirker søstjernernes evne til at åbne blåmuslinger. Det skal dog erindres, at netop i Løgstør Bredning var muslingernes fasthæftning svag (se afsnit 3.1), og tilsvarende

eksperimenter på en banke med solidt fasthæftede muslinger ville muligvis give et andet resultat.



Figur 11. Antallet af døde blåmuslinger i et bureksperiment i Løgstør Bredning (a) og i et akvarieeksperiment (b) med muslinger i intakt banke uden søstjerner (C), intakt banke med søstjerner (+S), og opløst struktur med søstjerner (-S) (V).

6.1 Størrelsesselektivitet

Undersøgelser af søstjerner's størrelsesvalg af muslinger har tidligere dokumenteret, at muslingerne kan opnå et størrelsesrefugie, hvor predationen ophører (Paine 1976). Felt- og laboratorieeksperimenter har vist, at søstjerner foretrækker at prede de mindre og mellemstore muslinger (O'Neill *et al* 1983, McClintock and Robnett 1986), men undersøgelserne er gennemført uden hensyntagen til muslingernes organisering i en bankestruktur. For at undersøge om søstjerner var i stand til at udvælge blåmuslinger fra bestemte størrelsesgrupper i muslingebanker, blev der indsamlet søstjerner, der var i gang med at åbne en blåmusling i Kaas Bredning (V). Størrelsen af de blåmuslinger, der var ved at blive prederet, blev sammenlignet med størrelsesfordelingen af hele muslinge populationen. Som det fremgår af tabel 2, var der på et par af stationerne to

størrelsesgrupper, hvoraf der ingen predation var på størrelsesgruppen af små muslinger. Hvis vi betragter predationen af de større muslinger, var deres størrelse større end populationens gennemsnitsstørrelse på to stationer, hvorimod det modsatte var gældende på to andre stationer.

		shell length (mm)					arm radius (mm)		corr.	
predated mussels		size class 1			size class 2			asterias		
mean	2 S.E.	Mean	2 S.E.	p_1	mean	2 S.E.	p_2	mean	2 S.E.	p_3
48.4	2.1	9.2	1.4	0.00	45.6	0.6	0.02	57.0	5.0	0.09
34.1	2.0	-	-	-	37.0	1.3	0.20	102.2	6.3	0.26
38.3	3.8	-	-	-	42.6	1.2	0.04	104.7	5.7	0.32
44.5	2.9	16.1	2.8	0.00	45.4	0.9	0.51	100.0	8.4	0.11
36.0	1.5	-	-	-	39.6	0.7	0.00	116.1	9.4	0.03
42.6	2.3	-	-	-	40.2	0.9	0.02	92.1	5.0	0.37

Tabel 2. længden af blåmuslinge populationerne (størrelsesgruppe 1+2), prederede muslinger og armradius af tilhørende prederende søstjerner. P-værdierne angiver signifikansen af t-tests, der teste om der er forskel mellem prederede muslinger og hele populationernes størrelsesfordeling (V).

7 Konklusion

I de tidligere afsnit er strukturene i en blåmuslingebanke beskrevet. Endvidere analyseres nogle af de mekanismer, der forklarer etableringen af bankestrukturerne. Muslingernes byssusfasthæftelse er et meget centralt strukturelt element i forståelsen af bankestrukturer og blåmuslingernes populationsdynamiske processer. I Limfjorden varierede enkelte muslingers fasthæftelse fra 115 g når fasthæftelsen ikke stimuleredes af tilstedeværelsen af søstjerner, *Asterias rubens*, og op til 900 g, når der var søstjerner tilstede. Også strømmen påvirkede blåmuslingernes fasthæftelse, men ikke indenfor det strømhastighedsinterval, der er karakteristisk for Limfjorden. Der blev på en fast sammenhæftet bank med søstjerner, målt morfologiske forskelle mellem muslinger indsamlet i øvre og nedre bankelag. Muslingerne i de øvre bankelag havde en større skallængde og kortere labial palper end muslingerne nederst i banken. Tilsvarende forskelle blev ikke målt på en løst sammenhængende bank uden søstjerner. Tilstedeværelsen af søstjerner er således vigtig for, hvor fast banken er sammenhæftet, samt om sammenhæftningen er så solid, at muslingernes position i banken fastholdes og vertikale morfologiske variationer kan udvikles. Undersøgelser af blåmuslingernes orientering i strømmende vand dokumenterede, at de ikke udviser nogen form for rheotaxi, altså orientering i forhold til en vandbevægelse. Fordelen ved en rheotaxisk orientering er begrænset af filtrationsapparatets fysiologi, der vanskeliggør en passiv filtrations-gevinst (Jørgensen 1990), og af det komplekse strømmønster, der vil opstå hen over en muslingebanke med stor ruhed. Endvidere vil en reorientering være

begrænset af muslingernes fasthæftelse. Muslingernes fasthæftning var ikke direkte hæmmende for søstjernernes predation af muslinger ved lave fasthæftningsstyrker (115 g). Dog havde muslingernes orientering betydning for predationen. Fjernelsen af byssusbindingerne i en muslingebanke, medførte en reorientering af muslingerne væk fra den dominerende orientering med posterior siden opad. Dette besværliggjorde søstjernernes mulighed for at indtage en fordelagtig position på muslingen i forbindelse med åbningen af denne, og reducerede derfor søstjernernes predationsrate.

Bentiske filtratorer er i lavvandede kystområder en vigtig komponent i kontrollen af fytoplanktonnet (Cloern 1982, 1991, Officer *et al.* 1982, Loo og Rosenberg 1989). Fra danske kystområder er betydningen af følgende bentiske filtratorer undersøgt: børsteormen, *Nereis diversicolor*, i Odense Fjord (Riisgård 1991), ascidien *Ciona intestinalis* i Kertinge Nor (Petersen og Riisgård 1992, Riisgård *et al.* 1996) og blåmuslingen i Roskilde Fjord (Møhlenberg 1995). Officer *et al.* (1982) opstillede nogle kriterier for områder, hvor bentiske filtratorer kan forventes at kontrollere fytoplanktonnet. Området skal være lavvandet med en lille vandudskiftning og have en stor population af filtratorer. Endvidere skal der være en konstant eller lav fytoplankton-tæthed og høje koncentrationer af næringssalte. Nyere undersøgelser viser, at fytoplanktonbestandene ikke kontrolleres af bentiske filtratorer, hvis en rumlig adskillelse af filtratorer og fytoplankton opretholdes af lave opblandingsrater (Cloern 1991, Møhlenberg 1995). I Løgstør Bredning blev der ved lav strømhastighed målt en reduceret fødeoptagelse i muslinger placeret i bunden af en muslingebanke i forhold til i de øverste bankelag. Klorofyl akkumulering var ligeledes lavere end i Kaas Bredning, hvor strømhastighed var højere, og der ikke var forskel i klorofyl indholdet i muslinger fra øverste og nederste bankelag. Muslingernes filtrations aktivitet kunne også aflæses i fordelingen af fytoplankton i de bundnære vandlag. Over begge banker reduceredes fytoplankton tætheden i bankeoverfladen til 1000 celler ml^{-1} . Reduktionen var tydeligst i Løgstør Bredning, hvor strømhastigheden og den resulterende vandopblanding var lav. Lave opblandingsrater af vandsøjlen medfører således en øget konkurrence om fødepartikler i en muslingebanke og en reduceret fjernelse af fytoplankton.

I Limfjorden foregår der et betydeligt muslingefiskeri, hvor 15% af bestandene fjernes årligt (VI). Fiskeriet af blåmuslinger i de indre danske farvande har skabt bekymring for, om fjernelsen af muslingebestandene lokalt reducerer den bentiske filtration og kontrollen af fytoplankton biomassen, med en forringet vandkvalitet til følge. Dokumentationen af, at muslingerne ved lave opblandingsrater er fødebegrænsede, indikerer derimod, at en reduktion i lokale blåmuslingebestande blot vil mindske den intraspecifikke fødekonkurrence, uden nødvendigvis at ændre bestandens filtrationen. Føde-begrænsningen medfører således, at en delvis fjernelse af bankens muslinger vil kompenseres af en øget filtration hos den enkelte musling. Muslingefiskeriet i Limfjorden er fordelt på 51 både, der fisker mere eller mindre samlet i et par områder af gangen. Fiskeriet kan fjerne op til 38 % af muslingerne i de enkelte fiskeriområder, men lokalt nedfiskes muslingebestandene næsten totalt og efterlader kun enkelte spredte muslinger. Set fra et filtrationsbiologisk synspunkt, er det stort set den dårligste udnyttelse af muslingeressourcen, man kan forestille sig, idet den totale fjernelse jo netop totalt eliminerer blåmuslingernes filtration. En delvis fjernelse af muslingebestandene og den medfølgende nedgang i filtrationspotentiallet vil derimod kunne kompenseres af de tilbageblevne muslinger, der vil øge deres filtration når føde-

konkurrencen reduceres. Som en yderligere gevinst vil muslingerne opnå en øget vækstrate og opbygning af biomasse, når fødeoptagelsen stiger. En optimal udnyttelse af muslingerne, der tilgodeser en hurtig vækst og en høj filtrationsrate, kræver nærmere undersøgelser af samspillet mellem flux af fødepartikler, fødeoptagelsen i muslingebanken, og de hydrodynamiske forhold.

Blåmuslingernes vækst er basalt set begrænset af deres fødeoptagelse, men forskelle mellem individuel længdevækst og væksten af størrelsesgrupper indikerer, at størrelsesspecifik mortalitet modulerer muslingernes gennemsnitsstørrelse både i sommer- og vinterperioden. I sommerperioden var væksten af størrelsesgruppen af blåmuslinger større end væksten af individuelt mærkede muslinger. Undersøgelserne i Løgstør Bredning i maj 1997 viste, at muslingerne nederst i muslingebanken havde en lavere fødeoptagelse end muslingerne øverst i banken, og den lavere energiindtagelse fører til en lavere vækst som observeret i Kaas Bredning. Da fødeoptagelsen er korreleret med opblandingsraten af vandsøjlen, vil en sommerperiode med lave vindstyrker og stor solindstråling øge fødebegrænsningen (Møhlenberg 1995) og øge dødeligheden af små muslinger i nederste bankelag. Muslingernes øgede vækst i sommerperioden vil endvidere forøge deres størrelse og dermed skærpe fødek konkurrencen. Også bankernes respiration vil kunne øge dødeligheden af små muslinger i de nederste bankelag. Jørgensen (1980) viste, at iltindholdet over en bank faldt fra bankens kant og ind mod centrum. Undersøgelserne i maj 1997 viste et konstant iltindhold ned gennem banken, men i situationer med en lille opblandingsrate af vandsøjlen, vil der opstå lave iltkoncentrationer over banken, og da iltforbruget er stort i banken fra respirerende muslinger og sediment, vil iltindholdet reduceres yderligere ned gennem banken. En øget dødelighed af små muslinger nederst i banken kan således forventes efter perioder med lille omrøring af vandsøjlen og lave iltkoncentrationer i bundvandet.

I vinterperioden blev der målt en længdereduktion i muslinge-populationerne, hvorimod de individuelt mærkede muslinger havde en lille vækst. Undersøgelserne af søstjernernes størrelsesseleksion af muslinger viste, at søstjernerne på visse muslingebanker præfererede blåmuslinger, der var større end muslingepopulationens gennemsnitsstørrelse, og der ingen predation var af helt små muslinger. Undersøgelserne af muslingernes vertikale størrelsesfordeling viste, at det kun var de øverste 30 % af muslingerne i banken, der var større. Søstjernerne vil derfor kunne fjerne disse yderste muslinger, hvorefter deres størrelsesvalg af muslinger vil afspejle populationernes gennemsnitsstørrelser.

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Makrostrukturen af muslingebanker

The structure of *Mytilus edulis* beds: effects of small-scale seston distribution.

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Abstract - Mussels, *Mytilus edulis*, gain advantage of living in beds in form of suitable and stabilised substrata, but have to struggle with intraspecific competition for space and food. The distribution of phytoplankton, particles (organic and inorganic) and oxygen was measured in vertical profiles within and above two mussel beds (-5 - 200 cm above the bottom) and related to food-uptake and hydrodynamic patterns. A declining near-bottom concentration of phytoplankton was measured at both stations. The largest decline was observed at station (B) that had a low mixing-rate of near bottom water. At both stations the phytoplankton concentration at the surface of the mussel bed approximated a threshold of 1000 cells ml⁻¹. Below this concentration mussels are reported to reduce feeding activity. At station (B) a reduced accumulation of chlorophyll *a* was observed in stomachs from mussels sampled in the lower layer in the mussel bed. It is assumed that the low turbulent mixing-rate reduced the transport of phytoplankton into the mussel bed, and since biomixing does not compensate for the reduced transport a reduced ingestion and chlorophyll accumulation could be observed. At station (A) no difference in chlorophyll accumulation was measured, and a larger mixing-rate was supposed to support a homogen filtration-rate in both the upper and lower layers. The effect of the reduced food uptake in the lower layer of a mussel bed was elucidated. Firmly mutually attached mussels formed the bed at station (A) and mussels in the upper layer were larger than mussels in the lower layer. No difference in shell lengths between upper and lower layers was observed when the mussels were loosely interattached as at station (B). No difference in shell weight or dry-weight (AFDW) was observed between mussels sampled in upper and lower layers at any of the two stations. At station (A) the inner labial palps were longer in mussels in the lower layer than in mussels in the upper layer. The labial palps are used to sort food particles and the larger size of labial palps was correlated to an increased near-bottom particle load.

Introduction

In the 1960' and early 1970' it was suggested that benthic suspension feeders were not food limited whereas deposit feeders were anticipated to be controlled by the food source. Levinton (1972) hypothesised that the suspension feeders do not compete for food because of a high variability in their food supplies and therefore they were not trophically specialised. The deposit feeders have a more constant food supply and he expected that this constancy induce a trophic specialisation through competition. Ólafsson (1986) confirmed the hypothesis in an exclusion experiment showing that growth of deposit feeding populations of *Macoma balthica* from a sheltered muddy sand sediment were density dependent, which were not the case in suspension feeding populations from an exposed sandy sediment. Other studies on food limitation in *Mytilus edulis* demonstrated that benthic filtrators reduce the seston concentration in the near-bottom layer (Fréchette & Bourget 1985a, Asmus & Asmus 1991) reducing the growth in *M. edulis* (Fréchette & Bourget 1985b, Small *et al.* 1986, Petersen *et al.* 1997).

For colonial species it has been difficult to judge if food or space is the limiting resource (Buss 1979). For the same reason food and space were claimed to be interdependent in benthic suspensions feeders (Buus 1979, Ólafsson 1986). Fréchette and Lefaivre (1990) established a

numerical model for populations of benthic suspension feeders in order to test if self-thinning was food- or space-driven. Experiments with *M. edulis*, kept in series of flow-through chambers, separating the food and space-limiting factors demonstrated that they were not interdependent (Fréchette *et al.* 1992).

The amount of food particles not only controls the food-uptake in benthic suspension feeders. Seston is a mixture of digestible organic particles and inorganic particles without food value. Laboratory experiments indicate that clearance and growth are increased in blue mussels feeding on a mixture of algae and suspension of silt (Kiørboe *et al.* 1981). The labial palps are used in selection of energy-rich food particles from the seston. Kiørboe and Møhlenberg (1981) analysed the separation efficiency of phytoplankton from silt in ten suspension feeding bivalves. They observed a correlation between interspecific palp-sizes adjusted for clearance capacity and the selection efficiency. Theisen (1982) measured a conspecific variation in morphometric characters in mussels from Danish waters, and observed a correlation between amount of suspended matter and labial palp sizes.

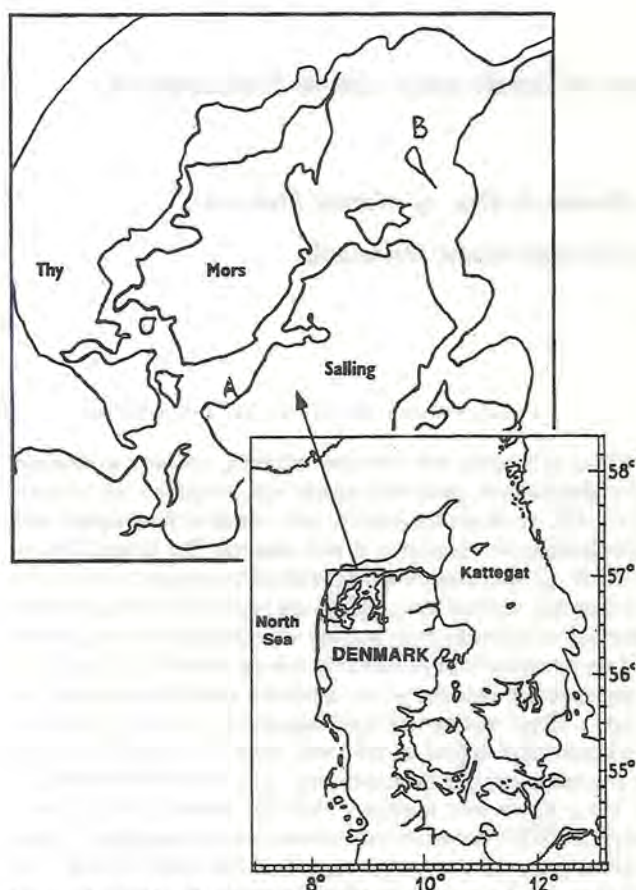


Fig. 1. Map of Limfjorden showing the positions of station (A) and station (B)

Mussel beds form complex tridimensional matrices of mutually attached mussels. Studies by Newell (1990) and Svane and Ompi (1993) showed that *M. edulis* at the edge were significant larger than mussels in the centre of mussel beds. Alvarado and Castilla (1996) observed that the mussels, *Perumytilus purpuratus*, were significant larger in upper bed layers compared to lower layers in mussel beds in Chile due to a greater number of intermediate sized mussel in the lower layer. Kausky (1982) measured similar high densities of smaller mussel in the lower layers of beds of *M. edulis* in the archipelago at the East Coast of Sweden, where smaller mussels are competitively suppressed by larger mussels. In periods with favourable food conditions or increased mortality of larger mussels, smaller mussels increase growth and replace the larger mussels. The observed horizontal and vertical size differences in mussel beds can be induced by ¹⁾ differences in growth caused by food-depletion of mussels in the centre or in the lower layers of the mussel beds, ²⁾ differences in recruitment patterns or ³⁾ differences in natural mortality (Alvarado and Castilla 1996).

In a previous study, the growth of *M. edulis* was analysed (Dolmer, in press). During winter, a small increment in shell length was observed at individual marked

mussels, whereas a significant size reduction was observed in the population of mussels. During summer, the population growth was larger than individual measured mussels. The observed growth patterns were hypothesised to be linked to a vertical size differences in mussel beds coupled to a size specific predation of *Asterias rubens* in winter (Dolmer, in press) and a size specific natural mortality induced by food-scarcity or oxygen stress in summer. This study describes the vertical structures of mussel beds, and analyse the feeding habitat parameters and oxygen conditions in two mussel beds.

Methods

The investigations were conducted in Limfjorden (Fig. 1), a 1575 km² Danish sound open to the North Sea in west and to the Kattegat in east. The sound is eutrophic because of nutrient- rich freshwater run-off from the watershed. A predominately western - eastern directed current combined with mixing of freshwater and saltwater induce a polyhaline salinity gradient ranging from 32 ppm in the western part to 18 ppm in the eastern part of the area. The vertical size structure of mussels in beds, the food uptake of the mussels and the phytoplankton and oxygen profiles inside and above mussel bed were measured at two stations. Station (A) and (B) were located in the western and the eastern part of the area, respectively (Fig. 1). The mean depths of water were eight metres at both stations.

Hydrodynamic conditions

Water flow was recorded continuously in two hours before sampling at both stations by a Braystoke current flowmeter 200 cm above the bottom. In order to measure the size of the boundary layer the flow was measured during 24 hours before sampling at station (B) by use of plaster cones (Muus 1968, Thompson and Glenn 1994) kept on an iron rod 12, 45, 78 or 112 cm ($n=2$) above the seabed. The flow speeds were estimated from the weight loss in the field by use of a calibration curve obtained from flume experiments. An average friction velocity (u_*) was estimated by the profile technique (Nowell *et al.* 1981) by fitting the measured flow velocities in the four heights above the bottom to a logarithmic velocity profile described as:

$$u = (u_*/\kappa) \ln(z/z_0)$$

where u is the horizontal velocity at height z above the bottom, κ is von Karmans constant (~ 0.4) and z_0 is the bottom roughness parameter estimates as $k_b/30$ where k_b is the mean length of the mussels in the bed (Butman *et al.* 1994). k_b was in the model assumed to be 3 cm.

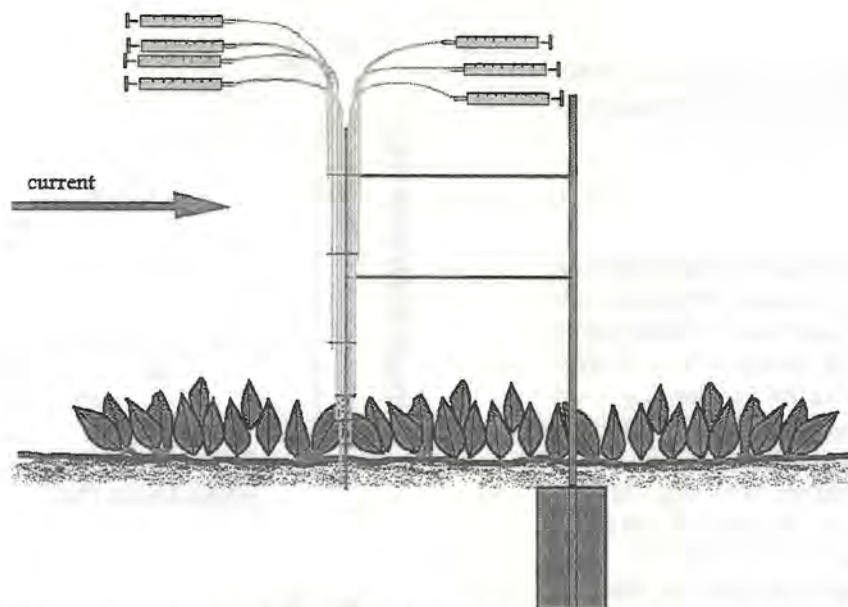


Fig. 2. The water sampling device fixed at a holder in the sea-bottom. The sampling device penetrates the mussel bed and 25 ml samples were obtained through a system of plastic pipes (diameter: 0.3 cm). Sampling heights were 5, 2.5 and 0 cm below the mussel bed surface and 2.5, 5, 10, 25, 50 cm above the mussel bed. Furthermore, two samples were taken 100 and 200 cm above the bottom. A diver operated the system and in order to avoid perturbation of the sampling spot the sampling device was orientated up-stream in relation to holder and diver.

Vertical description of mussels in upper and lower layers

Size distributions of mussels collected in the upper and lower layers of the mussel beds were described at both stations. A frame (25 x 25 cm) was pushed down through the mussel bed by a SCUBA diver, and a knife fitting into the frame separated the mussel bed in upper and lower layers. Eight samples were brought to the laboratory and total weight and shell lengths of all blue mussels in upper and lower layers were measured. The dry weight (AFDW) and shell weight of 20 mussels in upper and lower layers were measured at each station. In addition, the length of the inner labial palps was measured at 12 mussels from each layer at the stations.

The size distributions of mussels collected in the upper and lower layer at the two mussel beds (A and B) were analysed by a nested analysis of variance (ANOVA), with position in the mussel bed nested to sample. In order to handle unbalanced sets of data a GLM-procedure was used. The dry-weight, shell weight and length of labial palps at mussels were analysed as a function of position in the mussel bed by use of analysis of covariance (ANCOVA), with shell length as covariant. In the analyses of dry-weight and shell weight the data was ln-transformed. Before the tests, data were tested by F_{\max} tests to ensure homoscedasticity.

Distribution of food particles and oxygen

The concentrations of food particles and dissolved oxygen were measured from water samples ($n=3$) taken by a SCUBA diver through a system of plastic pipes (diameter 0.3 cm) penetrating the mussel beds (Fig. 2). The water samples were sucked up by syringes in vertical transects 200, 100, 50, 25, 10, 5, 2.5 and 0 cm above the bed and 2.5 and 5 cm below the bed surface when appropriate. First, 10

ml samples drained the pipes for surface water, and second, a 25 ml sample was sucked up and quickly transported to the surface. Samples with a visible content of sediment were rejected from further analysis. The amount of dissolved oxygen was measured by a standard Winkler titration method (Parsons *et al.* 1984); and a 10 ml subsample was preserved by addition of formalin. In the laboratory the density of particles and density and size of phytoplankton cells was measured. The density of particles was counted by a coulter counter (Elzone 180, orifice size 120 μm). The phytoplankton cells were counted in epifluorescence microscope after staining by acridine orange and concentrated on a 1.0 μm filter (Microclear, polycarbonate, black paint). Phytoplankton biomass was quantified as the amount of chlorophyll a at the stations. Water samples from two and six metres depth above bottom were filtrated through a GF/F filter. Plant pigments were extracted in 90% acetone before spectrophotometric measure of the chlorophyll a concentration (Parsons *et al.* 1984).

Mussel food uptake

In order to correlate the recorded near-bottom phytoplankton distribution to mussel ingestion in upper and lower bed layers, the amounts of chlorophyll a in blue mussel stomachs were measured. By use of the frame previously described, mussels were sampled in the upper and lower layers in the mussel beds at the two stations. The stomachs of 18 mussels from the upper and lower layers were dissected out and the plant pigments were extracted in 90 % Acetone. After 48 hrs, the concentration of chlorophyll a in each stomach was measured.

spectrophotometrically as described by Parsons *et al.* (1994). The effect of position in the mussel bed at the chlorophyll content was tested by two one-way ANOVA's.

Results

Hydrodynamic conditions

The water flow was recorded by a Braystoke currentmeter at station (B) from two hours before sampling of blue mussels for the stomach content analysis, and from 24 hours before by flume calibrated plaster balls arranged in a vertical profile. The velocity 200 cm above the sea bed (u_{200}) was measured by the Braystoke current meter to 2.6 cm sec^{-1} . A logarithmic velocity profile was fitted to the flow measurements obtained by the plaster balls (Fig. 3). The model explained 96.7 % of the variation in measured velocities and u_{200} was estimated to be 3.3 cm sec^{-1} . The friction velocity (u_*) was estimated to 0.18 cm sec^{-1} . At station (A) the Braystoke currentmeter recorded u_{200} to 4.5 cm sec^{-1} and a logarithmic velocity profile fitted to the flow record estimated the friction velocity (u_*) to 0.24 cm sec^{-1} .

Vertical description of mussels in upper and lower layers

The structure of the mussel bed differed between the two stations in respect to biomasses and sizes of mussel. Thickness of the mussel layer was at both stations 8-10 cm. At station (A) in the western part of the area the biomass of *Mytilus* was $734 \pm 63 \text{ g m}^{-2}$ (AFDW). The mean shell length ($\pm 2 \text{ S.E.}$) of the mussels was $43.5 \pm 0.4 \text{ mm}$. The relative shell length difference between mussels collected in the upper and lower bed layers was correlated ($p < 0.05$) to the fraction of mussels in subsamples from the upper layer in the mussel bed (Fig. 4a) - a low fraction correspond to a bed

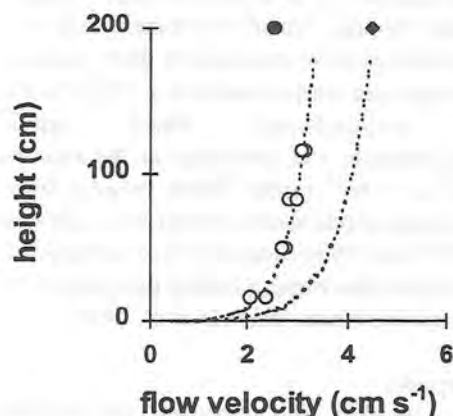


Fig. 3. Measured (o) vertical flow profile at station (B) by use of plaster cones. The measurements are fitted to a logarithmic velocity profile (dashed line - $R^2 = 96.7\%$) and the friction velocity was estimated ($u_* = 0.18 \text{ cm sec}^{-1}$). The water flow was recorded 200 cm above the bottom by a Braystoke current meter (●: station (A); ◆: station (B)). A logarithmic velocity profile was fitted to the Braystoke current measurement (solid line) at station (A) and the friction velocity was estimated ($u_* = 0.24 \text{ cm sec}^{-1}$).

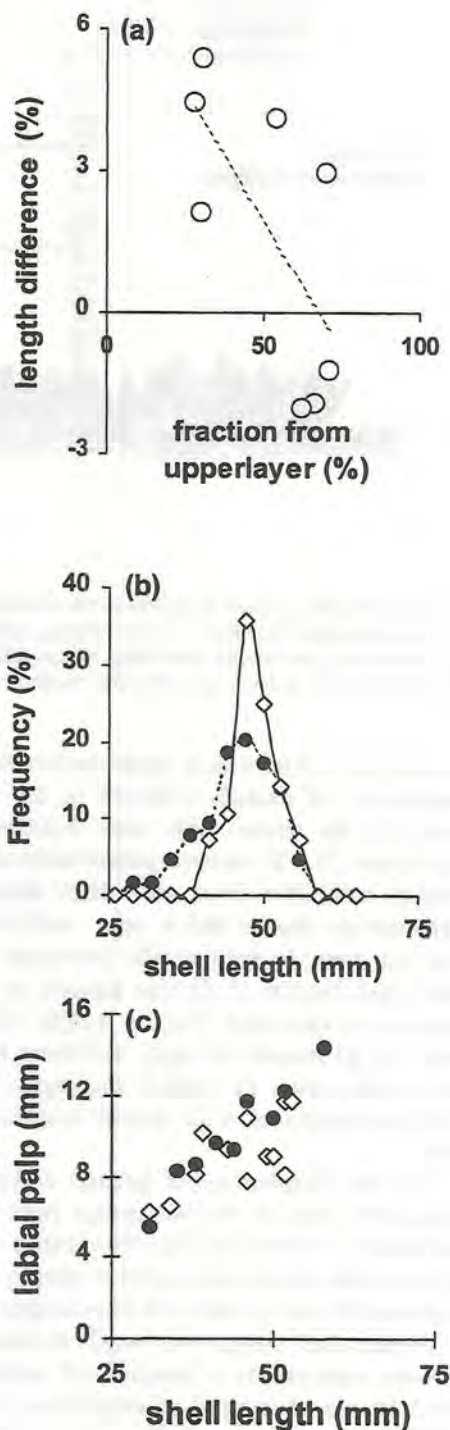


Fig. 4. The stratification of mussel morphology in a mussel bed at station (A). a) The relative difference in shell length between mussels in the upper and lower bed layers as a function of the separation-depth between upper and lower layers, measured as fraction of mussels in the upper layer subsample. b) Shell length distribution of mussels sampled in upper layer (◇) and lower layer (●). c) Length of the inner labial palps at mussels sampled in upper layer (◇) and lower layer (●).

Table 1. Nested ANOVA testing the shell-lengths of *Mytilus edulis* at station(A) and (B) as a function of sample number and position in the mussel bed nested to sample.

(A)

Source	DF	Seq SS	Adj SS	Adj MS	F	P
Sampel	2	1318.44	1217.55	608.77	9.15	0.052
Position(sampel)	3	199.64	199.64	66.55	2.97	0.032
Error	277	6203.46	6203.46	22.40		
Total	282	7721.54				

(B)

Source	DF	Seq SS	Adj SS	Adj MS	F	P
Sampel	7	1658.48	1430.74	204.39	4.67	0.022
Position(sampel)	8	349.84	349.84	43.73	1.61	0.119
Error	692	18829.80	18829.80	27.21		
Total	707	20838.13				

separation close to the surface. The three samples with the smallest fraction of mussels collected in the upper layer (upper fraction~30%) was tested further. A nested ANOVA, analysing the shell lengths as a function of vertical position in the mussel bed nested to the three samples, indicated that there was no difference between samples (Table 1, $p=0.052$), whereas a significant effect of the vertical position in the mussel bed was obtained (Table 1, $p=0.032$). The size distributions of mussels from the upper and lower layers show that the frequencies of larger mussel were identical in the two layers, whereas the frequencies of smaller mussels were higher in the lower layer (Fig. 4b). At station (B) in the eastern part of the area the blue mussel biomass was $302 \pm 45 \text{ g m}^{-2}$ (AFDW). The mean shell length ($\pm 2 \text{ S.E.}$) of the mussels was $43.3 \pm 0.4 \text{ mm}$. No correlation was observed between shell length differences between mussels in upper and lower layers and the fraction of mussels in the samples from the upper layer. A nested ANOVA testing the effects of sample and vertical position in the mussel bed indicated a significant effect of sample (Table 1, $p=0.022$), but no effect of vertical position in the mussel bed (Table 1, $p=0.119$).

The shell- and meat-weights (AFDW) of mussels collected in the upper and lower bed layers were at both stations significantly correlated to shell length ($p=0.000$), but not to the vertical position in the mussel bed ($p=0.379$ - 0.958). The length of inner labial palps in mussels at station (A) were significantly affected by the vertical position in the mussel bed ($p=0.044$) and were significantly correlated to the shell length of the belonging mussels ($p=0.000$). The mean length ($\pm 2 \text{ S.E.}$) of inner labial palps was $9.1 \pm 1.1 \text{ mm}$ at mussels sampled in the upper bed layer, whereas the length of labial palps in mussels in the lower layer was $9.9 \pm 1.4 \text{ mm}$ (Fig. 4c). The length of the inner labial palps at mussels sampled at station (B) were not affected by vertical position in the mussel bed ($p=0.717$), but only correlated to

shell length ($p=0.001$). The mean lengths of labial palps ($\pm 2 \text{ S.E.}$) from the upper and lower layers of mussels were $9.9 \pm 0.8 \text{ mm}$ and $10.4 \pm 0.9 \text{ mm}$, respectively.

Distribution of food particles and oxygen

The vertical distribution of phytoplankton cells were at both stations analysed by linear regression: $C_z = C_0 + dz$, where z is the height above the mussel bed, C_z is particle concentration in height z , C_0 is phytoplankton concentration at the surface of the mussel bed ($z = 0 \text{ cm}$), and d is the slope. At both stations a significant decline in concentration downward to the bed was observed (Fig. 5). The concentration of phytoplankton 200 cm above the mussel bed (C_{200}) was at station (A) $2650 \text{ cells ml}^{-1}$, whereas the concentration at station (B) was $5665 \text{ cells ml}^{-1}$. The concentrations at the surface (C_0) at (A) and (B) were 767 and $982 \text{ cells ml}^{-1}$, respectively. The mean size ($\pm 2 \text{ S.E.}$) of the counted phytoplankton cells were at (A) and (B) 6.2 ± 0.8 and $5.5 \pm 0.3 \mu\text{m}$, respectively. The mean sizes were not correlated to height above the mussel bed. The concentrations of chlorophyll a at two and six meters above the bottom were at (A) 1.4 and $1.8 \mu\text{g l}^{-1}$, respectively, and at (B) 3.2 and $4.4 \mu\text{g l}^{-1}$, respectively. The total number of particles measured by coulter counter was constant at both stations (Fig. 6). The mean particle density ($\pm 2 \text{ S.E.}$) was at station (A) $1075 \pm 178 \text{ particles ml}^{-1}$, whereas the density at (B) was $1246 \pm 373 \text{ particles ml}^{-1}$. At both stations a constant oxygen concentration was measured in vertical profiles above the bottom (Fig. 7). At station (A) and (B) the mean concentration ($\pm 2 \text{ S.E.}$) was 9.3 ± 0.1 and $7.0 \pm 0.1 \text{ mg O}_2 \text{ l}^{-1}$, respectively.

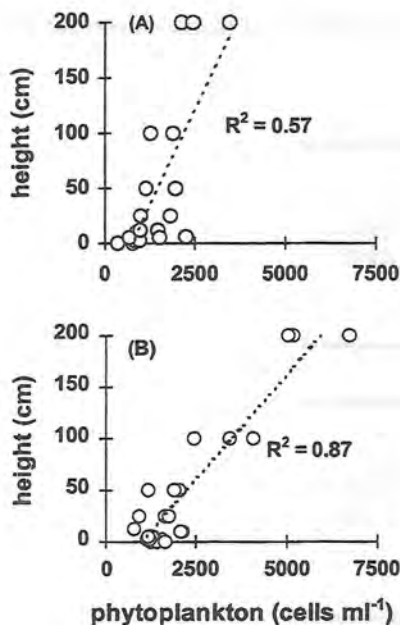


Fig. 5. Vertical profile of phytoplankton at station (A) and (B). The phytoplankton was counted in epifluorescence microscope. A linear regression: $C_z = C_0 + dz$ (z : height above the mussel bed, C_z : particle concentration at height z , C_0 is phytoplankton concentration at the surface of the mussel bed, d is the slope) was fitted to the measurements. C_z was 767 and 982 cells ml⁻¹ at station (A) and (B), respectively, whereas the slope was 14 and 25 cells cm⁻¹, respectively.

Mussel food uptake

The blue mussels at the two stations accumulated chlorophyll at different rates. At station (A) no difference was observed in chlorophyll content between upper and lower bed layers (One-way ANOVA, $p=0.960$). The mean chlorophyll content in stomachs (± 2 S.E.) were 30.3 ± 7.4 and $30.1 \pm 5.7 \mu\text{g}$ in mussels collected in upper and lower layers, respectively (Fig. 8). At station (B) a significant difference was observed between upper and lower layers (One-way ANOVA, $p=0.020$). The mean chlorophyll contents in mussels in upper and lower layers were 17.7 ± 4.7 and $11.3 \pm 2.6 \mu\text{g}$, respectively (fig. 8).

Discussion

Blue mussels, *M. edulis*, form epibenthic patches at hard and soft substrata and establish, especially on soft substrata, this form stabilised substrata for conspecific settlers (Young 1983, 1985). Mussels pay a cost for its aggregated distribution. Mussels are reported to reduce the amount of seston in the near-bottom water (Frechette & Bourget 1985a, Asmus & Asmus 1991) and thereby reduce the growth (Frechette & Bourget 1985b, Small *et al.* 1986, Petersen *et al.* 1997). Growth is further reduced in centre of mussel beds (Newell 1990, Svåne & Omipi 1993). Another cost of living in a patch is the induction of space-interference between individual mussels. Frechette *et al.* (1992) showed that growth of mussels was influenced by

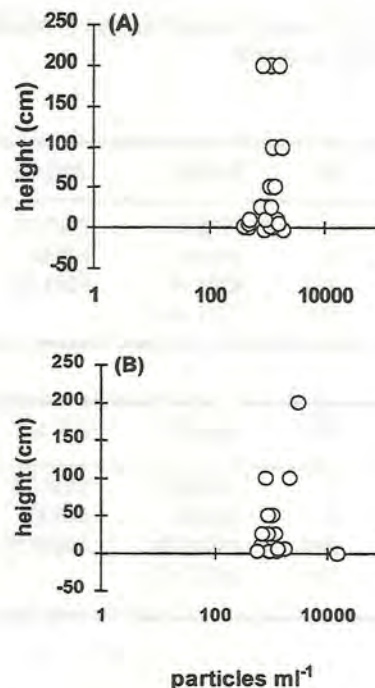


Fig. 6. Vertical profile of particles at station (A) and station (B) measured by coulter counter.

density of mussels and anticipated that external pressures at high conspecific densities reduce the gap size of the mussels. Since the gap size affects the pumping rate, reduced gap sizes constrain the food uptake (Jørgensen *et al.* 1988).

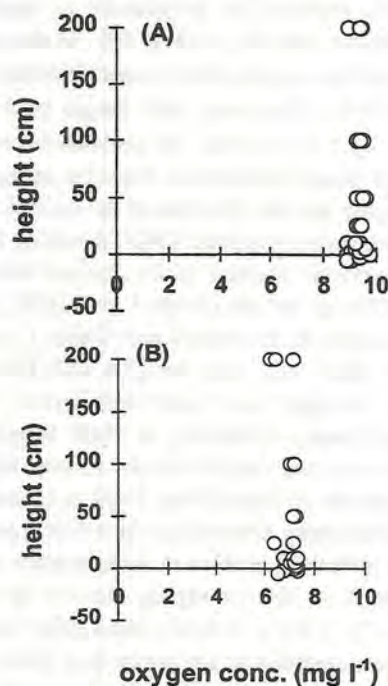


Fig. 7. Vertical oxygen profile at station (A) and station (B).

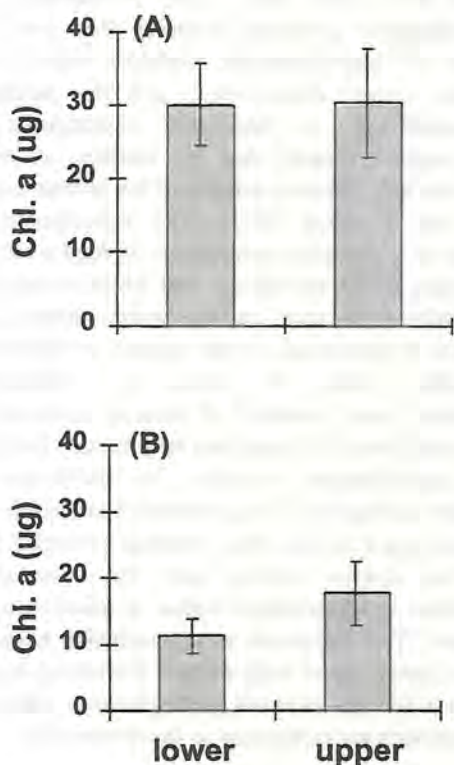


Fig. 8. Chlorophyll *a* content in mussels from the lower and upper layer in mussel beds at station (A) and station (B).

The mussels form a tridimensional matrix of byssus-thread interattached mussels. The strength and formation of the mussel bands is affected by several factors such as season (Price, 1980), size of mussels (Lee *et al.*, 1990), salinity, temperature, exposure to air, chemicals (van Winkle, 1970), substratum type (Young, 1983; 1985), current (Dolmer and Svane 1994) and position in a mussel bed (Witman and Suchanek, 1984). Witman & Suchanek (1984) showed that more force is required to dislodge mussels at the edge of mussel beds compared to at centre of the mussel beds on hard substrata. This observation can be explained by the tendency of mussels to form multilayered beds. The mussels at the edge form a strong attachment to the primary substratum, whereas mussels in the centre form a weaker attachment to adjacent mussels. Alternatively, mussels at the edge are more affected by flow and are stimulated to a stronger attachment. In a laboratory study, Martella (1974) observed that *M. edulis* produce more byssus threads when kept in clumps than individually kept mussels. This observation was explained by a tactile stimulation of the mussels when their foot was in contact with other conspecific mussels. Also, the presence of other species is reported to stimulate attachment. In a previous study a correlation between mussel attachment-strength and density of the predator, *Asterias rubens*, was observed (Dolmer, in press). At station (A), in the present study, a high density of starfish, *A. rubens*, (2.5 indiv m⁻¹) was correlated to a firm inter-attachment (900 g

of the mussels. At station (B) no starfish was observed and the mean attachment was 115 g. The correlation was confirmed in field- and laboratory-experiments where the attachment was stronger in mussels kept in cages or aquaria together with starfish than in mussels kept alone.

The strength of the attachment is important for the structure of the mussel bed. In beds with a firm interattachment, the mussels have a reduced ability to change their position or orientation (see also Dolmer *et al.* 1994). In this study a significant difference in shell lengths between mussels in upper and lower bed layers was observed at station (A), characterised by a firm bed structure. Only one size class of mussels was observed, and the frequency of smaller mussels was higher in the lower layer than in the upper layer. Furthermore, the labial palps in mussels in the lower layer were larger than palps in mussels from the upper layer. At station (B) characterised by loosely interattached mussels, no difference in shell lengths or labial palps were observed between the upper and lower layers. Stratification in the morphology of mussels may then first be detectable in beds of fixed mussels as at station (A).

The increased length of labial palps in mussel in the lower layers is an adaption to a higher load of inorganic particles (Kjørboe and Møhlenberg 1981, Theisen 1982). Particle counts (organic and inorganic particles) at the two stations indicated constant concentrations whereas the phytoplankton concentrations were declining downwards to the bottom. Consequently, the concentration of inorganic particles and other particles other than phytoplankton may increase close to the bottom. The range of the particle numbers were out of the range of the phytoplankton numbers, probably caused by formation of particle aggregations.

The establishment of colonial mussel beds induces an intraspecific competition for food and space (Fréchette *et al.* 1992). The amount of food available for suspension feeding benthic invertebrates is dependent on the concentration of seston but also on transport mechanisms. Suspended particles can either be transported to the near bottom zone above the mussel bed by turbulent mixing due to wind and current, or by horizontal advection. In a flume experiment Butman *et al.* (1994) measured a near-bottom seston concentration above an established mussel bed 4.7 metres from the leading edge. When the mussels were supplied with extra phytoplankton to the seawater (experiment 2) a clear near-bed depletion of fluorescence was measured in a 5 cm sec⁻¹ flow, whereas a less significant depletion was observed in a 15 cm sec⁻¹ flow. Two replica-experiments without extra addition of phytoplankton failed to show depletion. Also Muschenheim and Newell (1992) failed to demonstrate a depletion layer above a mussel

bed in a tidal channel eleven metres downstream the leading edge. The mean flow velocity was 9.8 cm sec^{-1} . Upstream, the mussel bed they measured highest concentrations of phytoplankton nearest the the bottom, whereas a more uniform distribution was measured above the mussel bed. In the present study a vertical declining phytoplankton concentration towards the bottom was measured at both stations. A more uniform vertical distribution was measured from the station with most turbulent flow (A), whereas a steeper concentration gradient was measured in more stagnant water (B). Møhlenberg (1995) measured a similar vertical declining concentration of chlorophyll in an estuary (5 metres of dept) at periods with low wind mixing. In periods with a well-mixed water column, a spatial homogen but temporal declining concentration was observed, as the phytoplankton was transported downwards to a filtering population of blue mussel. The two studies by Butman *et al.* (1994) and Muschenheim and Newell (1992) investigated near-bottom phytoplankton depletion in higher flow velocity conditions than in the present study. Furthermore, phytoplankton concentrations were measured in well-defined distances to the leading edge of the mussel bed. The mussel beds at the two stations in this study represents components of a complex mosaic of smaller and larger beds. As a consequence, the horizontal advection transports water which is partly depleted for food-particles by other parts of the mussel beds. The vertical turbulent mixing then serve as the main transport mechanism.

Butman *et al.* (1994) suggested that their experiment 1 and 3 failed to demonstrate a near bottom depletion of phytoplankton because of seston concentrations below a threshold, according to experiments by Thompson and Bayne, (1972). In the present study almost equal numbers of phytoplankton were counted at the surface of the mussel bed (A: $767 \text{ cells ml}^{-1}$; B: $982 \text{ cells ml}^{-1}$) despite of a large difference in concentration 200 cm above the bottom. In experiment 2, Butman *et al.*, (1994) supplied algae cultures of *Isochrysis galbana* and *Monochrysis lutheri* to the seawater in the flume. If we assume, that the fluorescence was the same for cultured algae and algae in the seawater, then a recalculation of upstream concentrations in experiment 1 and 3 yield a concentration of $1040 \text{ cells ml}^{-1}$, almost identical to the surface concentration (C_0) measured in the present study. Riisgård and Ramløv (1981) observed in laboratory filtration-experiments, that phytoplankton concentrations of *Phaeodactylum tricornutum* above 3×10^4 or below $1500 \text{ cells ml}^{-1}$ induce shell closure at *M. edulis* and thereby reduce the filtration. The measured phytoplankton concentrations at the surface of the mussel beds (C_0) at station (A) and (B) approximated the minimum threshold supporting filtration activity. At low transport-rates of food particles downward into the mussel bed the filtration and accumulation of chlorophyll diminish as observed at station (B).

Biomixing, induced by inhalent and exhalent siphonal flows, has to be considered as an important near-bottom mixing mechanism (O'Riordan *et al.* 1995). In their

model of phytoplankton depletion Butman *et al.* (1994) assumed that the effects of biomixing is negligible due to the small value of the filtration velocity relative to a typical boundary shear velocity. Modelling of phytoplankton depletion above the polychaeta, *Nereis diversicolor*, and the ascidian, *Ciona intestinalis*, in laboratory experiments in stagnant water indicated that the ascidian at weak current velocities induce a mixing of the bottom layers (Larsen and Riisgård 1997). The significance of biomixing as a transport mechanism of food particles may increase inside the mussel bed where turbulence is dampen from the near bottom layers increase the importance of biomixing. In the present investigation the feeding rates, in terms of chlorophyll accumulation, was measured at mussels collected in the upper and lower layers at two stations as a function of the hydrodynamic regimes. No difference in chlorophyll accumulation was observed at station (A) having the larger mixing rate, whereas at station (B), having the smaller mixing rate, the chlorophyll accumulation was significant higher in mussels in the upper layer. The difference in accumulation between upper and lower layers indicate that biomixing do not compensate for the reduced phytoplankton transport by external induced turbulence in the mussel bed.

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II

Dolmer, P. & I. Svane. 1994. Attachment and orientation of *Mytilus edulis* L. in flowing water. - Ophelia 40: 63-74



Filtrerende blåmuslinger.

ATTACHMENT AND ORIENTATION OF *MYTILUS EDULIS* L. IN FLOWING WATER

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ABSTRACT

The effects of flow velocity and shell orientation in a flow field on byssus thread attachment were investigated in the blue mussel *Mytilus edulis* L. in a flume flow. The number of established byssus threads and the strength of byssus attachment were significantly affected by flow velocity. No effect on number of attached byssus threads was observed relative to orientation of the mussel, but mussel orientation at termination of the high flow experiments was significantly dominated by the position: ventral upcurrent. By measuring the number of established byssus threads and the strength of attachment of individual detached byssus threads the potential strength of attachment was estimated. In still water the measured strength of attachment constituted 21% of the estimated potential strength of attachment, but in a 19.4 cm sec⁻¹ flow the measured strength of attachment constituted 81%. This observation indicates, that the correlation between the number of established byssus threads and the force of attachment is not a simple function.

The critical velocity at which a mussel was dislodged by flow was investigated as a function of mussel orientation. This experiment showed that the critical velocity was significantly affected by orientation of the mussel and shell height, where the orientations ventral and umbo upcurrent showed the highest critical velocities. No difference in drag was found between the orientations umbo upcurrent and ventral upcurrent, which were found to be the dominant orientations when mussels were kept in a flume flow, indicating orientations of low drag force.

INTRODUCTION

Living in a mussel bed in a low flow velocity habitat, the suspension feeding blue mussel *Mytilus edulis* L. have the filtration capacity to reduce the concentration of seston above the mussel bed (Frechette & Bourget 1985a, Asmus & Asmus 1991). This depletion of food may result in reduction of individual growth (Frechette & Bourget 1985b, Smaal et al. 1986). In turbulent flowing water the seston is renewed, but the mussels are exposed to hydrodynamic drag (Vogel 1981). To withstand drag and avoid dislodgement the mussels need mechanical attachment to the substratum at a metabolic cost. *M. edulis* is attached to the substratum by byssus threads.

The properties and function of *M. edulis* byssus threads have been described by Smeathers & Vincent (1979) and Waite (1983). The strength of the byssal attachment in the field varies as a function of season (Price 1980), size of the mussel, temperature, salinity, exposure to air, persistence of some chemicals (Van Winkle 1970), and substratum type (Glaus 1970, Young 1983, 1985). The byssal attachment is reported to increase in strength in mussels living in turbid water (Mahéo 1970, Glaus 1970, Witman & Suchanek 1984). In addition, Witman & Suchanek (1984) observed that greater force was needed to detach mussels at the edge of a mussel bed than in the center. However, mussels at the edge of a patch are generally larger than at other locations within a patch (Svane & Ompi 1993).

The morphology of the mussel shell may influence the drag on a mussel. By changing orientation in a flow-field, by a passive or an active process, the drag changes (Dyer 1986), and by changing the drag on the mussel the need for byssal attachment changes. If the mussel is orientated in a low drag position, the metabolic cost of byssus production can be reduced and allocated to other life processes increasing the fitness of the mussel.

In laboratory experiments Lee et al. (1990) have shown that the number of reattached byssal threads is a function of mussel size, and at any one current (10, 15 and 20 cm/s) there was an inverse relationship between mussel size and the rate of attachment. Furthermore, Lee et al. (1990) showed that for mussels kept in still water the combined strength of byssus threads increases with mussel size and that relationship between single thread strength and mussel size appears to be linear. However, Lee et al. (1990) did not consider effects of drag influenced by mussel orientation.

The aim of the experiments was to analyse the effect of a unidirectional water flow and mussel orientation on the strength of attachment and numbers of byssus threads produced by *M. edulis*. Furthermore, effects of direction of flow on re-orientation of mussels, and critical velocity as a function of the orientation were investigated.

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MATERIAL AND METHODS

In two series of flume experiments the attachment and orientation of *M. edulis* were analysed in April 1993 in a closed circuit flume flow (300 cm long, 48 wide, and 21 cm deep) situated at Kristineberg Marine Research Station, Sweden. The design of the flume is described by Vogel (1981). The mussels used in the experi-

ments were collected at 9 meters of depth at the location Björnsholm, a high-energy epibiosis in Strömmarna, on the west coast of Sweden. Mean flow velocities at 25-35 cm/s were measured on the location (see Dolmer et al. 1994).

Experiment I: Byssal attachment and orientation

The byssal attachment of *M. edulis* was tested as a function of the two factors flow velocity (3 levels) and start orientation of the mussel (4 levels). All 12 treatments were replicated 5 times in a random design. A rectangular glass plate (46 × 84 cm) was placed on the flume bottom with the edge 146 cm from the inlet. In each flume run 4 mussels were placed on the glass plate within a 30 cm long and 20 cm wide outlined quadrangle with the front 198 cm from the inlet. The start orientation of the mussels was chosen randomly from the four categories: umbonal region upcurrent or downcurrent, and dorsal or ventral region upcurrent (Fig. 1). Before each flume run, fresh seawater was added to the flume and the temperature recorded. The mussels were kept 24 hours in the flume in still water or with water-flows of 7.7 or 19.4 cm sec⁻¹, respectively. At the end of each flume run, the orientations of the mussels and the temperature were recorded. The glass plate with the attached mussels was subsequently moved to a table. By use of a spring balance, lifted by an electrical winch, the force needed to detach each mussel was measured. The force working on the mussels was increased by 17 g sec⁻¹. After detachment of the mussel, the number of byssus threads was counted. The force needed to detach individual byssus threads was measured on 5 or fewer threads. Each thread was fixed to the balanced spring by use of a small alligator clip and detached by use of the electrical winch. The length, height and width of the mussels were measured. The size range of the mussels used in the experiment was 64-88 mm, and the temperatures in the flume runs were observed to be in the range 6-14°C.

Experiment II: The critical flow velocity as a function of orientation of unattached mussels

In order to estimate the optimal orientation of a mussel in relation to flow, the flow velocity resulting in dislodgement or reorientation of unattached *M. edulis* was measured as a function of mussel size and orientation. Two length ranges of *M. edulis* were used: 60-70 mm and 80-90 mm. The same four different start orientations of the mussels as in experiment I were used: umbonal region upcurrent or downcurrent, and dorsal or ventral region upcurrent (Fig. 1). A total of 8 treatments (2 size groups, 4 orientations) was replicated 5 times in a random design (40 flume runs). On the glass plate used in experiment I, a circle (diameter 8 cm) was outlined 230 cm from the flume inlet. At the start of each flume run, one *M. edulis* was placed in the circle in one of the start orientations. The flow was in-

creased to 20 cm sec^{-1} , and every minute the flow was further increased 5 cm sec^{-1} in successive steps to a maximum velocity of 60 cm sec^{-1} . The velocity inducing the first movement of the mussel, and the critical velocity (dislodgement of the mussel from the circle or a reorientation for more than one minute) were recorded. If the mussels were reorientated, the new orientations were recorded. After each flume run, length, width and height of the mussel was measured.

DATA ANALYSIS

Experiment I:

Byssal attachment and orientation

The strength of byssal attachment was analysed as number of byssus threads attached in a 24 hour period, and as the force needed to detach a mussel. Two separate analyses of variance (Sokal & Rohlf 1981) were used to test attachment as a function of flow velocity and start orientation. Since the data met the demands for homoscedasticity (F_{MAX} -test: $p > 0.05$) they were not transformed. The means were compared by SNK-test (Zar 1984).

The final orientation of the mussels after 24 hours in the flume was tested with a G-test (Sokal & Rohlf 1981) assuming a random orientation.

By knowing the strength of attachment and the number of individual byssus threads for each mussel, it was possible to estimate the potential strength of attachment. This was defined as the detachment force necessary to detach all the byssus threads at the same time. By use of simple linear regression the measured strength was compared to the estimated potential strength of attachment based on data from the 3 flow velocities. The slopes and elevations were compared between the regressions based on data from 19.4 cm sec^{-1} and still water experiments by use of t-tests (Zar 1984). The regression for the 7.7 cm sec^{-1} data was not compared with the two other groups because of a small range of estimated strength.

Experiment II:

The critical flow velocity as a function of orientation of unattached mussels

The flow velocities, at which the first shell movement and the critical velocity was observed, were analysed in two separate analyses of covariance (Sokal & Rohlf 1981). The velocities were tested as a function of two factors: shell length and orientation. The heights of the shells were used as a covariate. The data were not transformed since they met the demands of homoscedasticity (F_{MAX} -test: $p > 0.05$). The means were compared by SNK-tests (Zar 1984).

The orientation of the mussels just before dislodgement from the test circle or after a reorientation was tested against a random distribution by use of a G-test (Sokal & Rohlf 1981).

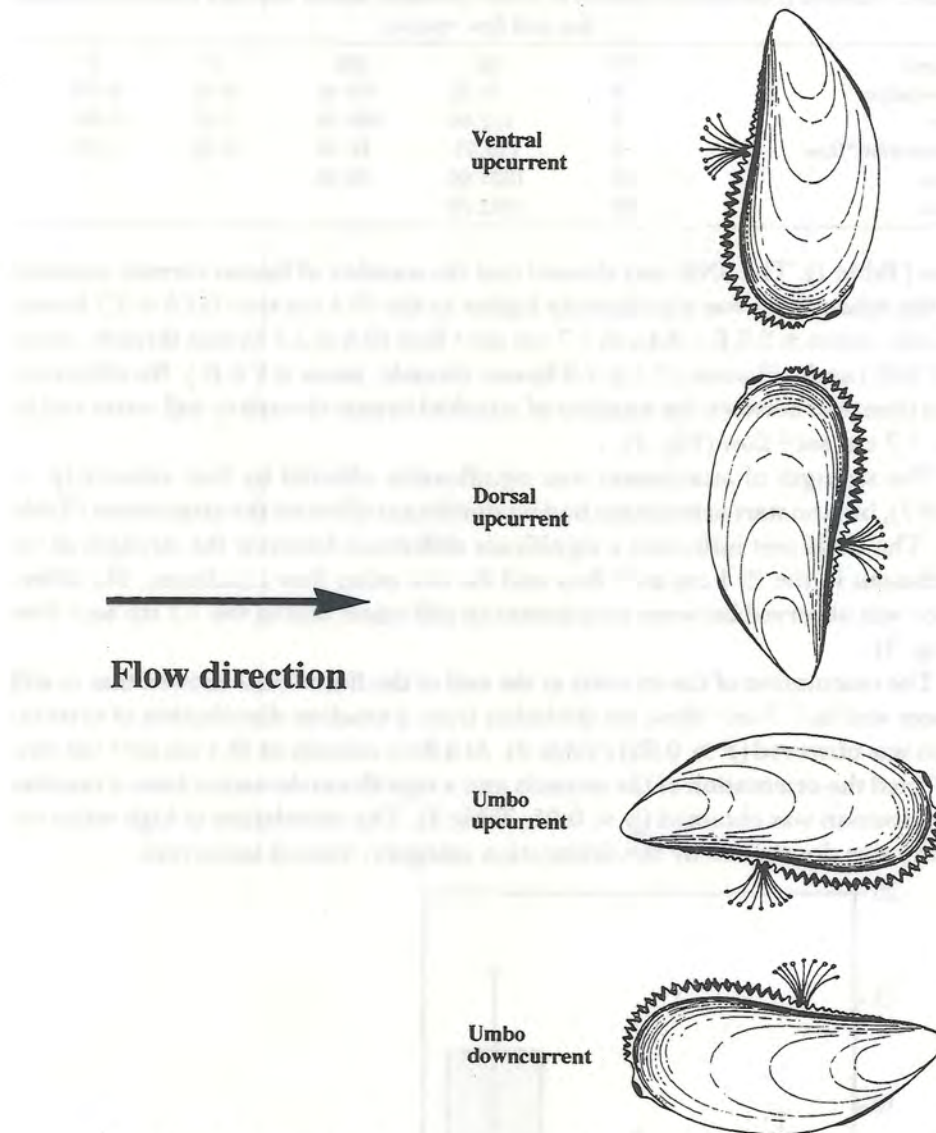


Fig. 1. The four categories of start orientations of *Mytilus edulis* (observed from above) in relation to the direction of water flow.

RESULTS

Experiment I: Byssal attachment and orientation

The number of byssus threads attached to the glass plate by the mussel was significantly affected by flow velocity ($p = 0.007$), but unaffected by start orientation.

Table 1. Analysis of variance on number of byssus threads in *Mytilus edulis* as a function of orientation and flow velocity.

Source	DF	SS	MS	F	P
orientation	3	76.32	25.44	0.67	0.575
flow	2	412.90	206.45	5.43	0.007
orientation*flow	6	128.03	21.34	0.56	0.759
error	48	1825.60	38.03		
total	59	2442.85			

tion (Table 1). The SNK-test showed that the number of byssus threads attached to the substratum was significantly higher in the 19.4 cm sec⁻¹ (12.6 ± 3.7 byssus threads, mean ± 2 S.E.) than in 7.7 cm sec⁻¹ flow (6.6 ± 2.2 byssus threads, mean ± 2 S.E.) and still water (7.7 ± 2.0 byssus threads, mean ± 2 S.E.). No difference was observed between the number of attached byssus threads in still water and in the 7.7 cm sec⁻¹ flow (Fig. 2).

The strength of attachment was significantly affected by flow velocity ($p = 0.007$), but the start orientation had no significant effect on the attachment (Table 2). The SNK-test indicated a significant difference between the strength of attachment in the 19.4 cm sec⁻¹ flow and the two other flow conditions. No difference was observed between attachment in still water and in the 7.7 cm sec⁻¹ flow (Fig. 3).

The orientation of the mussels at the end of the flume runs showed that in still water and in 7.7 sec⁻¹ flow, no deviation from a random distribution of orientation was observed ($P > 0.05$) (Table 3). At a flow velocity of 19.4 cm sec⁻¹ the flow affected the orientation of the mussels and a significant deviation from a random distribution was obtained ($p < 0.05$, Table 3). The orientation at high water velocity was dominated by the orientation category: ventral upcurrent.

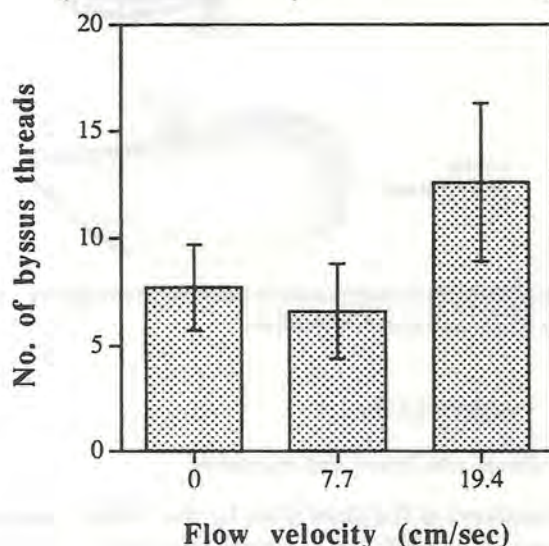


Fig. 2. The mean number a byssus threads attached by *Mytilus edulis* to a glass plate after a 24 hour period as a function of flow velocity (mean ± 2 S.E.).

Table 2. Analysis of variance on strength of byssus threads in *Mytilus edulis* as a function of orientation and flow velocity.

Source	DF	SS	MS	F	P
orientation	3	123541	41180	1.17	0.332
flow	2	394132	197066	5.59	0.007
orientation*flow	6	398068	66345	1.88	0.103
error	48	1692080	35252		
total	59	2607821			

The potential strength of attachment was estimated for all mussels where attachment of two or more byssus threads was measured. The potential strength of attachment was estimated as the number of established byssus threads times the mean of the individual byssus thread detachment force. A simple regression analysis indicated a linear relationship between the estimated potential strength and the measured strength of attachment for the data from still water and flows of 7.7 and 19.4 cm sec⁻¹ (Table 4). The slopes and elevations of the regression lines were significantly different comparing data from still water and a current velocity of 19.4 cm sec⁻¹ ($p < 0.001$) (Fig. 4). The slope of the regressions showed that in still water the measured strength of attachment constituted only 21% of the estimated potential strength, but in an 19.4 cm sec⁻¹ flow the measured attachment constituted 81%.

Experiment II: The critical flow velocity as a function of orientation of unattached mussels

The flow velocity at which the first shell movement was observed was not significantly influenced by mussel length and orientation, but only by shell height ($p =$

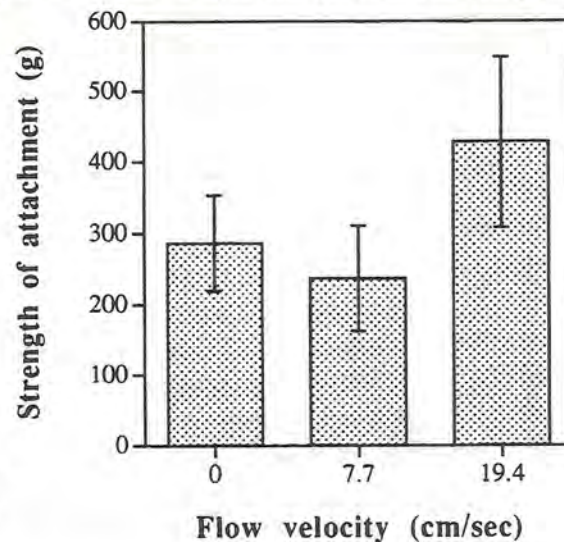


Fig. 3. The mean strength of byssus threads attached by *Mytilus edulis* to a glass plate after a 24 hour period as a function of flow velocity (mean \pm 2 S.E.).

Table 3. Analysis of orientation of *Mytilus edulis* as a function of flow velocity (G-test) n.s. = not significant, * = significant ($p < 0.05$).

Orientation	flow velocity (cm sec ⁻¹)			expected
	still	7.7	19.4	
umbo upcurrent	7	7	1	5
umbo downcurrent	4	3	3	5
dorsal upcurrent	3	4	2	5
ventral upcurrent	7	6	14	5
G _{adj} -value	4.6	2.1	18.8	
	n.s.	n.s.	*	

0.025, Table 5). The critical velocity was significantly affected by orientation of the mussel ($p < 0.000$) and shell height ($p = 0.011$, Table 6). The critical velocities are shown as a function of orientation in Fig. 5. The SNK-test indicated that critical velocity did not differ significantly between the orientations umbo upcurrent and ventral upcurrent or between umbo downcurrent and dorsal upcurrent ($p > 0.05$, Fig. 5).

A G-test showed that the orientation of mussels just before dislodgement or after reorientation deviated significantly from a random distribution ($0.005 < p < 0.001$, Table 7). The mussels were predominantly orientated with the ventral region upcurrent or the umbonal region upcurrent.

Table 4. Linear regression ($y = ax + b$) of the measured strength of the byssus threads in *Mytilus edulis* as a function of the estimated potential strength.

	a	b	R ²	n
still water	0.21	34	65	17
7.7 cm sec ⁻¹	0.40	83	47	12
19.4 cm sec ⁻¹	0.81	35	88	15

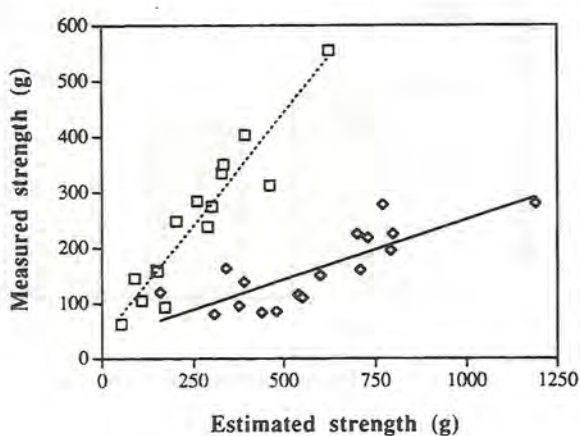


Fig. 4. The measured strength of byssus thread attachment in *Mytilus edulis* as a function of estimated potential strength. The solid line shows attachment to the substratum in still water and the dashed line in flowing water (19.4 cm sec⁻¹).

Table 5. Analysis of covariance of velocity for first shell movements in *Mytilus edulis* as a function of shell length and orientation, and with shell height as covariate.

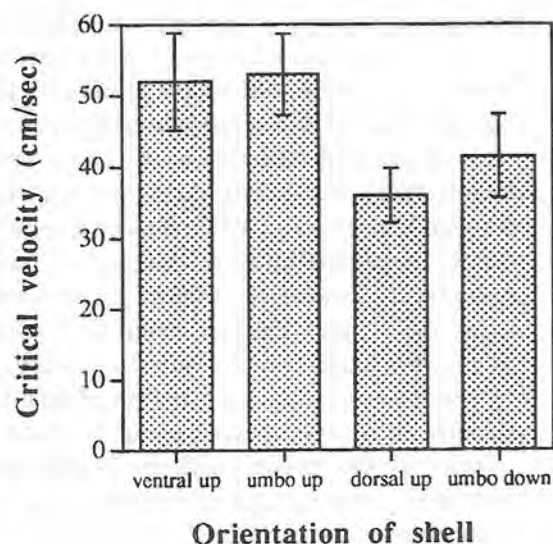
Source	DF	ADJ SS	MS	F	P
covariates	1	1086.9	1086.9	5.51	0.025**
length	1	639.2	639.2	3.24	0.082
orientation	3	1117.7	372.6	1.89	0.152
length*orientation	3	1024.5	341.5	1.73	0.181
error	31	6113.1	197.2		
total	39	9350.0			

Table 6. Analysis of covariance of critical velocity measured on *Mytilus edulis* as a function of shell length and orientation, and with shell height as a covariate.

Source	DF	ADJ SS	MS	F	P
covariates	1	1582.0	1582.0	7.41	0.011**
length	1	175.6	175.6	0.82	0.371
orientation	3	6445.1	2148.4	10.06	0.000***
length*orientation	3	1627.1	542.4	2.54	0.074
error	31	6618.0	213.5		
total	39	18637.5			

DISCUSSION

The blue mussel *M. edulis* is a quantitatively prominent bivalve in wave-swept environments. The approximative wing-shaped morphology of the shells lent themselves to hydrodynamic considerations since the mussels, attached by byssus threads to hard substrata, may experience a considerable drag. Field observations and laboratory experiments have shown an increase in the number of at-

Fig. 5. The mean critical velocity as a function of four orientations in *Mytilus edulis* (mean \pm 2 S.E.).

tached byssus threads and the force of attachment in habitats in turbid waters compared to habitats in still waters (Mahéo 1970, Glaus 1970, Witman & Suchanek 1984, Lee et al. 1990). However, none of these authors gave any importance to the orientation of mussels in relation to drag and flow directions. Since the response of a mussel to drag is increased byssal attachment, an orientation reducing drag may conserve energy and consequently increase fitness.

Our results confirmed previous studies showing an effect of flow velocity on both number of byssus threads and the strength of attachment. At high flow velocity an increased number of byssus threads and consequently a stronger attachment was observed. However, no effects of shell orientation in relation to direction of flow on the number of byssus threads or strength of attachment were obtained.

The estimate of potential strength of attachment based on measurements of individually detached byssus threads deviated from the actual measured detachment force. In still water the measured strength of attachment constituted 21% of the estimated potential strength. At a flow velocity of 19.4 cm sec^{-1} the measured strength of attachment constituted 81% of the estimated potential strength. Consequently, these observations indicated an increased utilization of the potential for attachment at increased flow velocity. However, the correlation between the number of established byssus threads and the force of attachment is not a simple function, but influenced by flow velocity and drag (see also Lee et al. 1990).

The formation and attachment of new byssus threads is described by Mahéo (1970) and Waite (1983). Since both the foot and the byssus retractor muscles are under nervous control, exogenous factors such as water movement can be assumed to influence the byssus formation rate and the choice of position for attaching byssus threads. However, Dolmer et al. (1994) was not able to demonstrate a rheotactic response affecting byssus thread attachment.

The orientation of mussels in a current may affect the food uptake and the removal of waste products (see Shimeta & Jumars 1991). A model study of bivalve siphons showed that a perpendicular orientation of the siphons in relation to a current reduced refiltration of water from the exhalent siphon (Monismith & Koseff 1990). Field observations of *Geukensia demissa* (Frey et al. 1987) and *Mya arenaria* (Vincent et al. 1988) showed a perpendicular orientation in locations with bidirectional tidal-induced currents. A passive orientation perpendicular to the current is reported from a flume study of empty shells of *M. edulis* (Kelling & Williams 1967). According to Vogel (1981) mussels should be expected to orientate themselves parallel to the flow direction to reduce the drag. Our analysis of the critical flow velocity as a function of orientation indicated no difference in drag between the umbo upcurrent and the ventral upcurrent orientation. The critical velocity for the mussels with the dorsal side upcurrent was lower than when the ventral side was upcurrent indicating that a dorsal region upcurrent orientation induces more drag than a ventral region upcurrent orientation. When orientated

Table 7. Analysis of orientation at the critical velocity in *Mytilus edulis* (G-test). * = significant ($p < 0.05$).

orientation	observed	expected
umbo upcurrent	13	10
umbo downcurrent	3	10
ventral upcurrent	7	10
dorsal upcurrent	17	10
G _{adj} -value	15.3*	

on a flat surface with the ventral side upcurrent, the shell tilts so that the exposed ventro-lateral surface constitutes a 45° angle to the flow direction thereby reducing the drag. When orientated with the dorsal side upcurrent, the dorso-lateral shell surface constitutes a 90° angle to the flow direction thereby inducing drag. The results showed that mussels in a 19.4 cm sec^{-1} current were orientated with the ventral side upcurrent. The byssus threads were used as an anchor and the mussels were passively moved to an orientation with the ventral side upcurrent. The orientation of the unattached mussels (experiment II) was not random. The orientations ventral region upcurrent and umbonal region upcurrent dominated the distribution of orientations indicating orientations of least drag. Consequently, when a mussel is dislodged, the drag force will turn the mussel to a low drag orientation preventing further transport.

In the field the local microtopography and interactions with other mussels interfere making an extrapolation of flume experiments to field situations difficult, but the results showed that an optimal position of a mussel in relation to flow direction exists combining shell morphology with byssus thread attachment thereby reducing drag.

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Errata

Re: P. Dolmer & I. Svane
Ophelia 40: 63-74 (1994)

Abstract:

On page 63:

"In still water the measured strength..... attachment is not a simple function."

Replaced by:

"In still water and in a 19.4 cm sec^{-1} flow no difference in the relation between measured and estimated strength was observed. The measured strength of attachment constituted 47 % of the potential strength of attachment".

Results:

On page 69:

"The slopes and elevations of the regression lines.....measured attachment constituted 81%."

Replaced by:

"The two regression lines were not significant different comparing data from still water and a current velocity of 19.4 cm sec^{-1} . (Fig. 4). The slope of a regression of the pooled data showed that the measured strength of attachment constituted 47 % of the estimated strength."

Table 4. Linear regression ($y=ax+b$) of the measured strength of the byssus threads in *Mytilus edulis* as a function of the potential strength.

	a	b	R^2	n
Still water	0.43	61	68	17
7.7 cm sec^{-1}	0.40	83	47	12
19.4 cm sec^{-1}	0.50	8	83	15

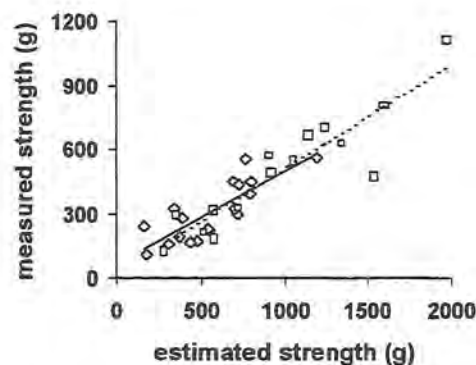


Fig. 4. The measured strength of byssus thread attachment in *Mytilus edulis* as a function of estimated potential strength. The solid line shows attachment to the substratum in still water and the dashed line in flowing water 19.4 cm sec^{-1} .

Discussion:

On page 72:

"In still water the measured strength of attachmentattachment at increased flow velocity."

Replaced by:

"In both still water and in the 19.4 cm sec^{-1} flow the measured strength of attachment constituted 47 % of the estimated strength."

III

Dolmer, P., M. Karlsson & I. Svane. 1994. A test of rheotactic behaviour of the blue mussel *Mytilus edulis* L. - Phuket Mar. Biol. Cent. Spec. Publ. 13: 177-184.



Tealia felina

A TEST OF RHEOTACTIC BEHAVIOUR OF THE BLUE MUSSEL *MYTILUS EDULIS* L.

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ABSTRACT

Many marine invertebrates show rheotaxis. Marine mussels may orientate the inhalant siphon towards currents to optimize feeding and sanitary conditions thereby improving growth rates. The blue mussel, *Mytilus edulis* L., forms extensive beds on both hard and soft substrata. *M. edulis* is an active filter-feeder showing great mobility by constant reorientation and attachment by aid of a well developed foot and byssus threads. We predicted that mussels would show rheotaxis and orientate uniformly in relation to currents to optimize feeding. To test this hypothesis, orientation of mussels in the field were observed using underwater stereophotography. Furthermore, experiments *in situ* and in a laboratory flume were performed. The results showed that *M. edulis* lack rheotaxis. Movements within a mussel patch were highly dynamic indicating that rheotactic behaviour may be concealed by the difficulty in experimentally separating competition for space from competition for food.

INTRODUCTION

Orientation of marine invertebrates in relation to currents is reported to be advantageous by inducing passive flow for filtration in sponges (Vogel, 1974), gorgonians and leptogorgonians (Wainwright & Dillon, 1980; Leversee, 1976), brachiopods (LaBarbara, 1977), scallops (Hartnoll, 1967), sabellid polychaetes (Merz, 1984), and ascidians (Young & Braithwaite, 1980). Field observations of the infaunal mussel, *Geukensia demissa* (Frey *et al.*, 1987), and *Mya arenaria* (Van Vincent *et al.*, 1988) showed a perpendicular orientation of the siphons relative to flow direction in locations with bidirectional tidal currents and in a model study of bivalve siphons, Monismith & Koseff (1990) showed that a perpendicular orientation in relation to flow direction reduced refiltration of water from the exhalant siphon. Eckman *et al.* (1989) showed that in the bay scallop, *Argopecten irradians concentricus*, changes in orientation relative to currents may provide a significant means of maintaining high growth rates.

The blue mussel, *Mytilus edulis* L., is influenced

by water movement throughout its life cycle affecting dispersal of gametes and larvae, renewal of food resources and oxygen, and removal of metabolic waste products (Frechette & Bourget, 1985; Butman, 1987; Asmus & Asmus, 1991; Shimeta & Jumars, 1991). Mussels living in still water may experience reduced growth rates (e.g. Svane & Ompi, 1993) and *M. edulis* and *M. californianus* living sympatrically are reported to reduce competition from other species by living in wave-swept environments (Suchanek, 1981). There are thus several factors which may influence behavioural adaptations in relation to currents and water flow. The question we want to address is: "Does the blue mussel, *M. edulis*, display rheotactic behaviour?". First, we made field observations by underwater stereophotography in a natural habitat with predictable high water flow. Second, we performed field experiments with orientation of mussels established in pre-fixed positions. Third, we performed experiments in a laboratory flume to study rheotactic behaviour in a unidirectional flow.

MATERIALS AND METHODS

The field observations and experiments were performed at Björnsholmen, a high-flow habitat constituting a man-made channel of 9 meter depth, 30 meter wide and 350 meter long situated in Strömmarna, an area of narrow sounds connecting Gullmarsfjorden with Koljöfjorden on the west coast of Sweden. The bottom of the channel is flat and covered with *M. edulis* coexisting with the small morph of the sea anemone *Metridium senile* (L.). The current in the channel is bidirectional and generated by a relatively small tidal amplitude (30 cm) and changing air-pressures. The current velocity may be as high as 100 cm/sec.

The flume experiments were conducted in a closed circuit flume flow (300 cm long, 48 cm wide, and 21 cm deep) situated at Kristineberg Marine Biological Station. The design of the flume is described by Vogel (1981).

Field observations of mussel orientation

Orientation of *M. edulis* was analysed by use of underwater stereophotography (see Lundälv, 1971; Svane & Gröndahl, 1988). A transect line with 8 regular spaced position marks was haphazardly placed on the bottom parallel to the channel walls in March 1993 and a stereophotograph was taken at each position mark. The stereocamera was equipped with a 50 x 50 cm photographic frame so the resulting photographs represented 8 replicates, each covering 0.25 m² of the mussel bed. The seawater temperature varied between 2-4 °C.

The orientation of the mussels in the stereophotographs was analysed in two aligned Wild M5 stereomicroscopes where a three-dimensional view of the mussels could be obtained. Only mussels with the umbo pointing downwards, when it was possible to identify the position of the sagittal plane, were included in the analysis. By use of a compass fixed to the photographic frame the orientation of the mussels was determined in relation to the direction of the flow. The orientations of the mussels were ranked in 8 classes of 45° sections out of 360°. Deviation from a random orientation was tested by use of a G-test (Sokal & Rohlf, 1981) comparing the 8 classes

of orientations against an even distribution. Since the mussels occupy a habitat with a bidirectional current the 8 classes were pooled in pairs, so that classes with an equivalent orientation in relation to the two directions of flow were reduced to one class, reducing 8 classes to 4. These 4 classes of orientations were compared to an even distribution by use of a G-test.

Field experiments on mussel orientation

In field experiments with high and low mussel density, the orientation of *M. edulis* was investigated as a function of initial orientation in relation to direction of flow. In both the experiments, plastic trays (36x54 cm) subdivided into 4 sections (18x27 cm), and separated by thin plastic walls, were filled with coarse sandy sediment.

The mussels used in the experiments were collected by scuba divers at the location Björnsholmen on the 16th of March 1993. Mussels in the length interval of 65-85 mm were used in the experiments. The mussels were cleaned of byssus threads and epizoids and kept at the laboratory in running seawater.

On the 22nd of March 1993, 6 sediment filled plastic trays (24 compartments) were placed on the bottom of Björnssund channel. In each tray section, 24 mussels were placed with the anterior end (umbo) into the sediment and one quarter of the mussel below the sediment surface. In each tray section, the mussels were oriented in the same direction. Four initial orientations were used with the sagittal plane orientated vertically 0, 90, 180, and 270° from the direction of the flow, respectively. The direction 0° was 240° compass reading. All four treatments were thus replicated 6 times in a randomized design. The trays were arranged on the bottom perpendicular to the prevailing direction of the current and buried down into the sediment level of the mussel bed. The trays were then stereophotographed immediately after deployment and subsequently after 24 and 48 hours. The photographs were analysed as described above.

The orientations of the sagittal plane of the mussels were ranked in 8 classes of orientation, and compared after 24 and 48 hours with the start distribu-

tion by use of two separate G-tests (Sokal & Rohlf, 1981). Deviations from initial orientations after 24 and 48 hours were tested using Kruskal-Wallis test (Zar, 1984).

During the field experiment, flow activity was measured by use of the technique described by Muus (1968). Two series of moulded plaster balls each attached to a 2 mm metal wire were fastened 12 cm above the edge of each tray. The subsequent erosion of the plaster balls was measured by weighing and the mean flow velocity calculated by interpolation of a flume calibration curve.

Flume experiments: reorientation as a function of flow

Orientations of mussels arranged in 6 x 4 blocks of mussels were investigated in two separate flume runs with flow velocities adjusted to 0 and 20 cm/sec, respectively. In each run, mussels were placed in a 35x35 cm sediment filled box in the recessed area of the flume, 200 cm from the flume inlet. In each flume run 24 mussels were arranged in identical positions in a 18x24 cm matrix in the center of the sediment box. The mussels were oriented as described for the field experiment with the anterior part (umbo) into the sediment with one quarter of the mussel below the sediment surface. The orientation of the sagittal plane were 0, 90, 180, 270° in relation to the direction of flow. Each treatment was replicated 6 times with different and freshly collected mussels. After 24 hours of exposure the mussels were photographed and the orientations subsequently recorded. Effect of orientation was tested in a one factor ANOVA using the computer package, SuperANOVA (Abacus v. 1.11) for Macintosh. Homogeneity of variances was tested by use of the F_{\max} -test (Sokal & Rohlf, 1981).

An identical experiment as described above was performed with only 2 mussels per flume run. The same four start orientations of the mussels were used and all treatments were replicated 6 times.

Flume experiments - gape size as a function of shell orientation and flow

Mussels in the size interval of 50-55 mm were col-

lected in natural mussel beds at Rønbjerg Marine Biological Field Station, Denmark, and placed in a sand filled PVC tube with an inner diameter of 42 mm and a length of 50 mm. Two tubes with individual mussels were positioned parallel and vertically to the flow direction in a sand filled box in the recessed area of the flume with the upper edge of the tubes leveled with the sediment surface. The mussels were placed in the sand of the individual tubes and orientated as described above. Two series of experiments with four shell orientations and two flow speeds were performed in a two-factorial statistical design. Each experiment was replicated 11 to 7 times. Gape sizes were measured on calibrated photographs taken after each flume run. The results were tested statistically using a two-factor ANOVA. Homogeneity of variances was tested by use of the F_{\max} -test.

Flume experiments - byssus tread application as a function of shell orientation and flow

These experiments were conducted as described above. Angle of attachment of byssus threads to the edge of the surrounding tube edge in relation to flow direction was measured after 30 minutes of flow or no flow. The data was tested statistically by use of two-factor ANOVA. Homogeneity of variances was tested by use of the F_{\max} -test.

RESULTS

Field observations of mussel orientation

The orientations of 297 mussels from the 8 transect stereophotographs were recorded. A G-test of orientation of the sagittal plane divided into 8 classes of orientation showed a non-significant deviation from a random distribution ($0.25 < p < 0.50$). When the 8 classes of orientation were pooled in pairs into 4 classes of orientation, considering the bidirectional flow conditions, a G-test also showed a non-significant deviation from a random distribution ($0.1 < p < 0.25$). The classes of orientations and the frequency of mussels in the classes are shown in Table 1.

Field experiments of mussel orientation

The mussels arranged in regular blocks in sediment filled trays deployed on the bottom of the

Table 1. Gape direction of vertically positioned *Mytilus edulis* L. in a natural mussel bed in Björnsund channel. 0 and 180 degrees indicate the main directions of the bi-directional currents. The observed values are not statistically different from a random distribution. Total number of mussels = 297.

Angle section	Frequency (%)	Angle section	Frequency (%)
1 0-45	12.1	1+5	26.6
2 45-90	15.5	2+6	30.6
3 90-135	15.2	3+7	25.6
4 135-180	8.8	4+8	17.2
5 180-225	14.5		
6 225-270	15.2		
7 270-315	10.4		
8 315-360	8.4		

Table 2. Reorientations of *Mytilus edulis* L. of more than $\pm 22.5^\circ$ deviation from initial orientation after 1 and 2 days. The reorientations are not significantly different from initial orientations (Kruskal-Wallis test; $p > 0.05$).

Day 1	Angle	No. of mussels	%	SD	Day 2	Angle	No. of mussels	%	SD
	0°	6	61.1	15.1		0°	6	82.7	4.9
	90°	4	45.4	21.4		90°	6	68.9	14.1
	180°	5	45.3	4.0		180°	6	71.9	7.0
	270°	5	47.7	7.6		270°	6	73.7	13.1
Total		20	50.7	14.1			24	74.3	11.2

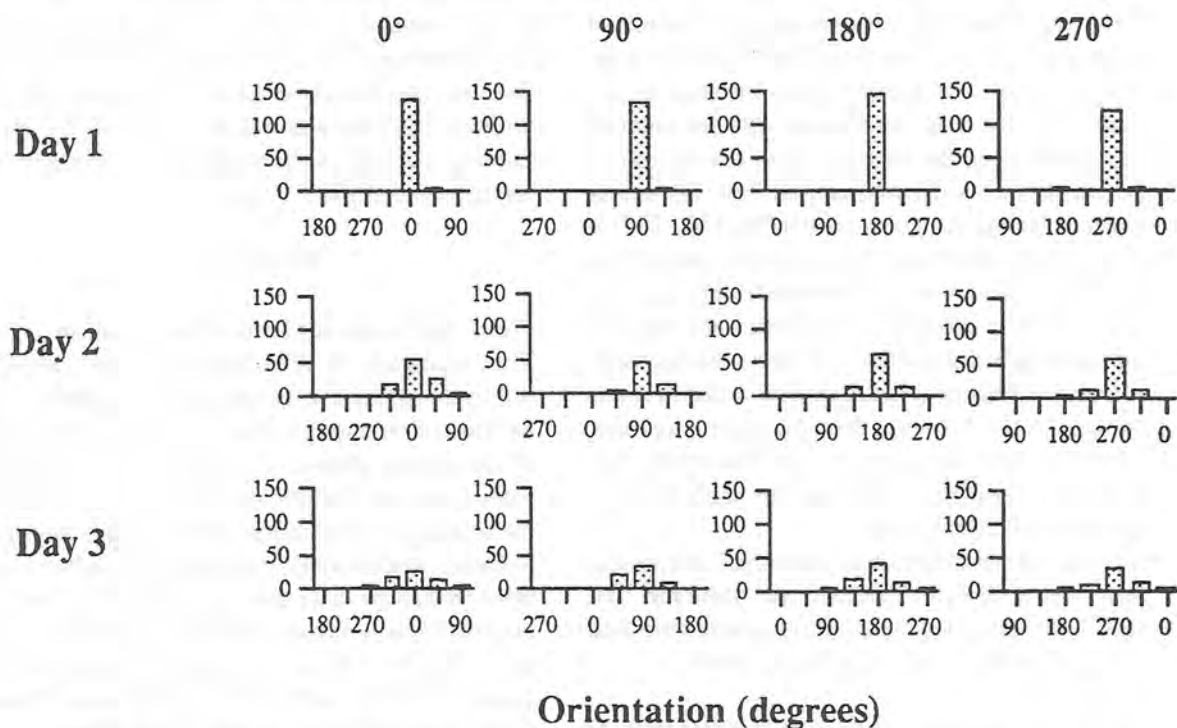


Figure 1. Distribution of orientations during a 48 hours experiment of preset orientated *Mytilus edulis* arranged vertically in blocks of 6x4 mussels in sediment in plastic trays exposed to bidirectional currents on the bottom of Björnsund channel.

Björnsholmen channel, reorientated from a regular preset distribution to a random distribution of orientations within two days. After 24 hours, no significant reorientation was observed (G-test, $p < 0.001$). After 48 hours a random distribution of orientations was obtained indicating that a significant reorientation of mussels took place (G-test, $0.1 < p < 0.5$). Fig. 1 shows the reorientations of the mussels as a function of time and initial orientation. The number of mussels reorientating more than $\pm 22.5^\circ$ from the initial orientations was not significantly dependent of initial orientation after 24 hours (Kruskal-Wallis, $p = 0.38$) or after 48 hours ($p = 0.185$) (Table 2).

During the experiment, the mean flow velocity was calculated to 25 cm/sec ($n=4$) the first 24 hours and 32 cm/sec ($n=2$) the second 24 hours.

It was not possible to perform experiments with solitary mussels distributed in sediment in trays since the individual mussels either moved away to the edges or were lost. In both field experiments, performed in May and later in September 1993 with only two mussels per tray section, most of the sediment was quickly eroded by the flow and most of the mussels were consequently lost.

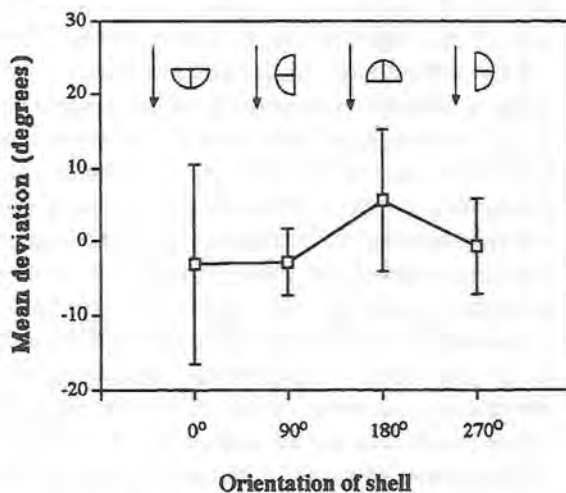


Figure 2. Mean deviation from preset orientations of vertically arranged blocks of 6x4 *Mytilus edulis* exposed to a flow velocity of 20 cm/sec in a laboratory flume. Flow direction and positions of mussel indicated above. Error bars indicate 95% significance level.

Flume experiments: reorientation as a function of flow

The orientations of mussels arranged in blocks at four different directions 24 hours after deployment are shown in Fig. 2. The mussels in each flume run showed only slight movements and fixed themselves to one another by byssus threads. No significant effect of initial orientation was found (one-way ANOVA, $p > 0.05$).

In the flume experiments with two mussels per flume run, none of the mussels exposed to 0 or 20 cm/sec were observed to reorientate from the initial orientation.

Flume experiments - gape size as a function of shell orientation and flow

Gape size in *M. edulis* was found to be independent of flow and initial orientation (Fig. 3). A two-factor ANOVA showed no significant effect of orientation to flow. However, there appears to be a tendency, although not statistically significant ($p = 0.08$), that gape sizes are larger during the flow conditions compared to conditions of no flow irrespective of initial orientations.

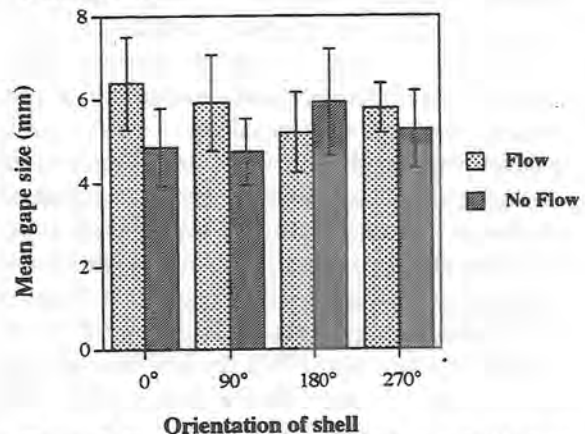


Figure 3. Gape size as a function of flow and preset orientation of *Mytilus edulis* arranged vertically in sediment filled PVC-tubes and exposed to flow of 0 & 20 cm/sec. Flow direction, positions of mussels, and error bars as in Fig. 2.

Flume experiments - byssus thread application as a function of shell orientation and flow

The patterns of directions of byssus thread applications are shown in Fig. 4. Mussels applied byssus

treads randomly irrespective of orientation of the individual mussels and flow conditions. A two-factor ANOVA showed no statistical effects of orientation ($p = 0.652$) or flow ($p = 0.628$).

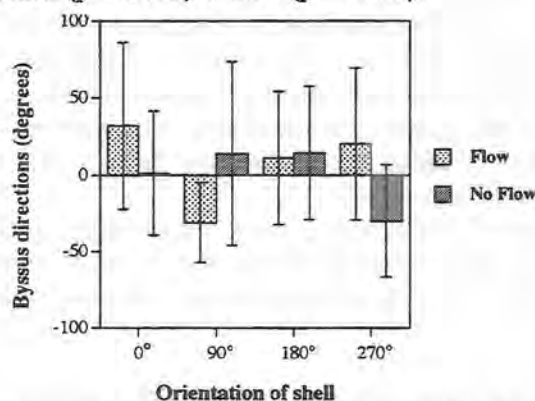


Figure 4. Directions of byssus thread application of pre-set orientated *Mytilus edulis* arranged vertically in sediment filled PVC-tubes and exposed to flow of 0 and 20 cm/sec. Flow direction, position of mussels, and error bars as in Fig.2.

DISCUSSION

There are theoretically several advantages for suspension feeding mussels to show rheotactic behaviour. The most important orientation may be to position the siphons with the inhalant siphon upcurrent and exhalant siphon downcurrent thereby taking advantage of induced passive flow and to release waste products downstream. When mussels are oriented with the inhalant siphon upcurrent, an increased hydrostatic pressure into the siphon can be observed. This increased hydrostatic pressure on the inhalant side of the gills results in a deflation of the demibranchs in *M. edulis* (Jørgensen, 1990). According to Jørgensen (1990), the deflation increases the resistance to water flow and reduce any effect of a passive current. The metabolic cost for active filtration in *M. edulis* has been calculated to be 1.5 % of the total aerobic metabolic rate (Jørgensen *et al.*, 1986) which is low. Hence, any energy gained by a passive flow would be likely to be lost by increased cost of movements to obtain a favorable position. Our results showed that under the experimental conditions in this study no rheotactic behaviour was evident in orientation and gape size thus rejecting the hypothesis.

Growth of scallops, *Placopecten magellanicus*, has been reported to be dependent on flow velocity by Wildish & Saulnier (1992). At high flow velocities (> 13.5 cm/sec) growth decreased. At lower flow velocities no effect was observed. Individual *M. edulis* located at the edge of a mussel bed are generally larger than in the center where mussels experience lower turbulence and flow rates (Suchanek, 1981; Newell, 1990; Svane & Ompi, 1993). The correlation of flow velocity and growth may be explained by favourable feeding conditions at high flow rates simply because more particles pass the siphons per unit time and not due to increased physical performance of the mussels.

In the epibenthic mussel *M. edulis*, the posterior byssal retractor muscle is located directly above the byssus root. This position allows a powerful anchorage to the substratum (Stanley, 1972). Our results showed that directions of byssus thread application was random, independent of flow and initial orientation. Consequently, direction of byssus thread applications were not an indicator of rheotactic behaviour. Young (1983) showed that *M. edulis* do not attach to sediment particles less than 0.85 mm in diameter by use of byssus threads. Assuming that mussels primarily use a byssal attachment and a tightening of the byssus threads controlled by the posterior byssal retractor muscle for movements, the use of sandy sediment may to some extent have prevented reorientation. In the flume experiments with solitary mussels, movements from the original positions were marginal indicating that access to hard substratum may be necessary for movements.

It was not possible to perform field experiments with individual mussels in the different tray compartments since the sediment was partly eroded away, some of the mussels were lost, and some were found attached on the edges. In the experiments with more mussels in the individual compartments, mussels quickly became interconnected by byssus threads which stabilized the blocks and the sediment thereby inhibiting rheotaxis. Witman & Suchanek (1984) observed in a mussel bed established on hard substratum that the byssal attachment was tighter on the edge of a mussel bed than in the center. Byssal threads in *M. edulis* may consequently have evolved for attachment, *per se*, and not for rheotactic orientation.

Our field observations showed that mussels, with respect to a bidirectional current, were distributed randomly. Constant movements and reorientations were observed during the experiments when a batch of mussels was used. In a mussel bed the local microtopography may induce a complex, changing flow field above the mussel bed (Frey *et al.*, 1987) thus obscuring a possible rheotactic pattern. Grant *et al.* (1993) found that passive transport of sea scallops had a behavioural component related to gape that is independent of shell size. Scallop orientation and recessing was explained by physical processes rather than simple behaviour (Grant *et al.*, 1993). The problem of interpreting behavioural movements in mussels is complex and strongly connected with

the problem of separating competition for space from competition for food.

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IV

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Søstjerner, *Asteria rubens* og søanemoner, *Metridium senile*

Seasonal and spatial variability in growth of *Mytilus edulis* L. in a brackish sound: comparisons of individual mussel growth and growth of size classes

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Abstract

Growth of *Mytilus edulis* L. in a brackish Danish sound was estimated from individually measured mussels and measurements of discrete size classes. In winter, individual mussels grew faster than size classes of mussels, and in summer, the inverse situation occurred. The effect of size-specific mortality of larger mussels in winter, and smaller mussels in summer on the population dynamics is discussed. Spatial variability in growth was analysed by comparing von Bertalanffy growth rates estimated for discrete size classes of mussels at different locations in the sound. Faster growth rates were measured in the western part of the sound characterised by a higher salinity and current speed. The observations were supported by results of cage experiments with individually marked mussels. © 1998 Elsevier Science B.V.

Keywords: Blue mussels; *Mytilus edulis*; Individual growth; Size class growth; Size-specific mortality

1. Introduction

Growth of the blue mussel *Mytilus edulis* has been extensively investigated because of its important economical and ecological role. Growth varies according to size, age, and genotype of the mussel; and is influenced by environmental parameters such as temperature, salinity, water movement, and concentration and quality of seston (see review by Seed and Suchanek, 1992).

Mussel growth can be measured on individually marked or caged mussels (Theisen, 1975; Kautsky, 1982; Page and Hubbard, 1987), or by reading of annual growth rings (Theisen, 1973; Berard et al.,

1992). Strömberg (1975) measured absolute growth of mussels in the laboratory using the laser diffraction technique. Alternatively, growth can be assessed by measuring the change in size distribution of recognisable cohorts in mussel populations (Bayne and Worrall, 1980; Kautsky, 1982; Page and Hubbard, 1987; Kautsky et al., 1990), but estimates obtained by this method are sensitive to size-dependent mortality in mussel populations (see Seed and Suchanek, 1992). Most growth studies of *M. edulis* analyse the growth of mussels kept in suspension in the water column (Kautsky et al., 1990; Riisgård and Poulsen, 1981; Stirling and Okumus, 1994). However, it is difficult to compare growth of benthic and pelagically maintained mussels because benthic mussels are reported to be food-limited, which can re-

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strict growth (Fréchette and Bourget, 1985a,b).

In Lim Fjord, Denmark there is an important fishery on natural stocks of blue mussels, with annual landings exceeding 100,000 tonnes. The minimum size of legally landed mussels is 4.5 cm (shell length), and knowledge of the production of mussels

is important for the management of the fishery. This study describes the spatial and seasonal variation in growth, based on growth rates of individually measured mussels and discrete size classes of mussels.

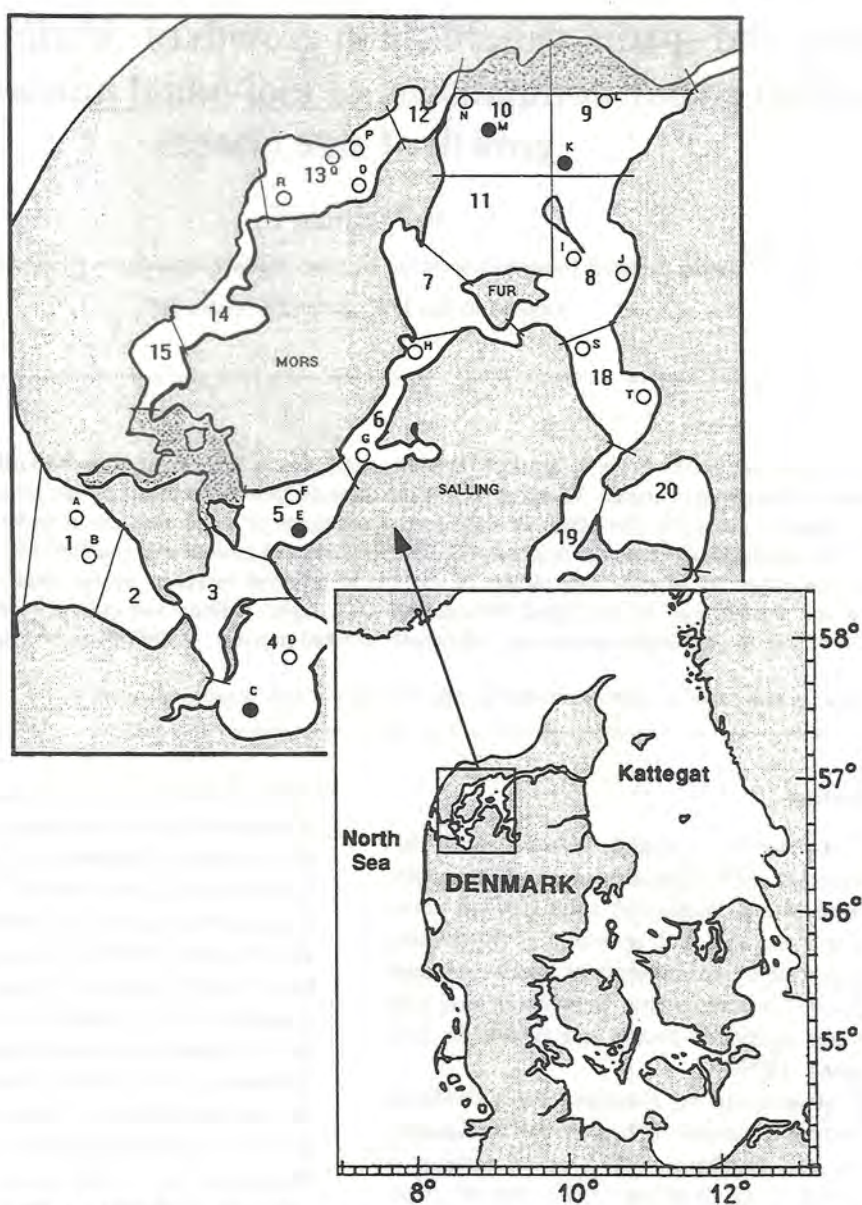


Fig. 1. A map of Lim Fjord showing the subareas (1–20). The circles marked by a letter show the positions of the stations used in 1995. The open circles indicate cage positions, and the black circles indicate cage positions and sampling positions for size class measurements. The darker areas indicate subareas closed for mussel fishery.

2. Methods

~~Limfjorden~~ ~~Lim Fjord~~ (Fig. 1) is a 1575-km² Danish sound open to the North Sea in the west and to the Kattegat in the east. The salinity ranges from 32‰ in the western part to 22‰ in the eastern part of the area. The sound is eutrophic, receiving nutrients from the surrounding areas and primary production is high, exceeding 1000 mg C m⁻² day⁻¹ in summer; this frequently induces oxygen depletion in the benthos, especially in the more enclosed parts of the area (Jørgensen, 1980).

2.1. Growth of size classes of mussels

~~Limfjorden~~ In January to December 1995, samples of mussels were dredged at four stations in ~~Lim Fjord~~ at 8–9 m of depth. The size distributions were monitored either bimonthly (stations C, E, M) or more regularly (station K: eight times; see Fig. 1). In January and April, mussels were sampled using a 1:2 scaled model of a commercial mussel dredge (mesh size 50 mm, towing speed 3 knots), and the rest of the samples were collected by a triangular dredge (mesh size 10 mm, towing speed 1 knot). The mean efficiency of the mussel dredge is 17%, and this increases with mussel biomass (Dolmer et al., in prep.). The efficiency of the triangular dredge was assumed to be 100% because of the low towing speed. After collection, the mussels were frozen and the shell length of about 300 randomly selected mussels from each station was measured in the laboratory.

2.2. Growth of individually marked mussels

~~Limfjorden~~ Growth of *M. edulis* was measured in three series of cage experiments at 16 stations in ~~Lim Fjord~~. In order to measure individual and local variability in growth, mussels were individually marked by engraving or by a Artline 440 xf paint marker. In order to avoid predation from starfish or crabs, the mussels were held in cages (30 × 60 cm, mesh diameter 2.1 cm) for six weeks in January to March, and for four weeks in July to August and November to December. One size group of 15 mussels was held in each cage in January and November (shell length 57 ± 2 mm and 44 ± 1 mm, respectively, mean ± 2 S.E.), and in July two size groups of 15 mussels (37 ± 3

mm and 56 ± 2 mm) were placed in each cage. One cage with mussels was used per station. Before and after the experiments, shell lengths were measured to the nearest 0.01 mm using a digital caliper.

The spatial variation in growth rates in January–March, July–August and November–December were analysed by three separate analysis of covariance (ANCOVA) with initial shell length as covariant. The growth data were balanced and ln transformed to homogenise variances.

2.3. Control experiments

In order to test for the effects of cages on mussel growth a series of control experiments was conducted at four stations in November–December (station J, K, N and O; Fig. 1). To avoid predation from starfish, stations with a low or zero density of *Asterias rubens* were identified by use of UV video and diver observations. Plates of slate (42 × 62 cm) were attached to the side of the cages at each of the four stations, and a diver was placed 15 marked mussels on each plate. Mussels on the plates were sampled after four weeks by diver and changes in shell length estimated as previously described.

2.4. Spatial variability in growth

As part of a stock assessment, mussels were sampled quantitatively at 362 stations in 18 subareas in ~~Lim Fjord~~ in May 1993 (Fig. 1). Samples were taken by use of an 1:2 scaled model of a commercial mussel dredge aboard the 20 GTR vessel 'Havfisken'. In May 1994, 317 of the stations were revisited and sampled. Shell lengths of ca. 100 mussels were measured to the nearest 0.5 cm on board the vessel. At 126 stations not influenced by fishing activity, which almost depletes local mussel populations, a single discrete size class was identified in both the 1993 and the 1994 samples, and the growth of the size classes between May 1993 and May 1994 was estimated at each station by comparing the change in mean lengths over the 12-month period. In order to test for spatial variability in growth, growth data were subjected to an analysis of covariance (ANCOVA) with mean length in 1993 and biomass (wet-weight) of mussels on each station as covariates. Some of the subareas were excluded from the

analysis because of inadequate data. Data from sub-areas 14–15 and 18–19 were pooled and afterwards, the matrix was reduced to obtain a balanced design ($n = 7$). The test data were transformed by the $\ln(x + 1)$ function to homogenise the variances.

3. Results

3.1. Growth of size classes of mussels

Limfjorden Growth of *M. edulis* in *Limfjorden* was measured at four stations. The average initial density of mussels (wet-weight) in January at the four stations was $2.2 \pm 0.5 \text{ kg m}^{-2}$ (mean ± 2 S.E.). The size classes on the size–frequency diagrams were discrete (Fig. 2), and the change in the mean length of the size classes of mussels measured. At station C, E, and K, a single size class of mussels was observed, and the growth increment was 19.4–22.7 mm in the period January to December, from an initial length of 17.6 to 26.8 mm (Fig. 3). An initial reduction in shell length was observed from January to March at stations C and E, and from January to April at station K. The reductions ranged from 0.45 to 3.5 mm. In addition, a reduction of mean size was observed at station E from November to December, which diver observations of the bottom disturbance suggested was related to the mussel fishery.

At station M, two size classes of mussels were observed. The mean length of the smaller size class was 9.2 mm in March increasing to 12.9 mm in December (Fig. 3). The larger size class had a mean length of 48.0 mm in March increasing to 51.9 mm in August, with a decrease in length from April to July. In August, an oxygen concentration of only 0.5 mg l^{-1} was measured in subarea 10 (data from the counties surrounding *Limfjorden*), and the larger size class disappeared.

3.2. Growth of individually marked mussels

at The growth of *M. edulis* held in cages was measured at 16 stations in January–March. The biomass (wet-weight) of the natural mussel populations ~~for~~ the stations with cages was $0.8 \pm 0.4 \text{ kg m}^{-2}$ (mean ± 2 S.E.). From January to March, the mean growth increment of mussels from all 16 cages

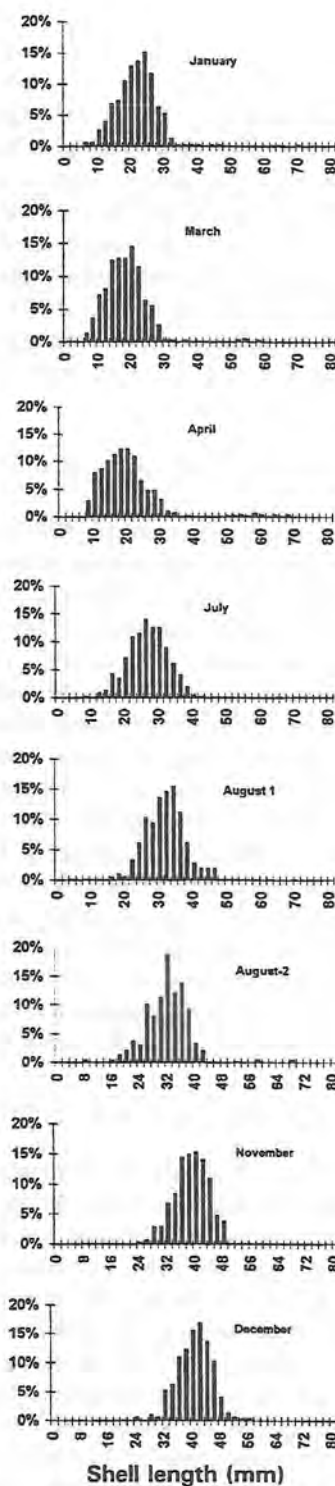


Fig. 2. Frequency distribution of *M. edulis* from station K.

was 0.12 ± 0.08 mm (mean ± 2 S.E.) from an initial mean length of 57 mm. The growth rate corresponded to 0.02 mm week⁻¹. The analysis of covariance (ANCOVA) testing for spatial variability in growth, by the initial length as covariant, indicated a significant spatial variation in growth rates among the 16 cages (Table 1, $p = 0.027$), but Turkey's test failed to identify the differences in growth rates.

From July to August, the cages in the western part of the sound (subareas 4–6) were fouled by settled ascideans. The mean growth of the larger mussels in all 16 cages was 0.13 ± 0.10 mm (mean ± 2 S.E.) from an initial mean length of 56 mm, or 0.03 mm week⁻¹. At four stations (D, E, F and J; Fig. 1), recognition of marks was impossible on many smaller mussels. At the remaining stations, mussels showed a mean overall growth of 1.98 ± 0.18 mm (mean ± 2 S.E.) from an initial length of 37 mm, or 0.50 mm week⁻¹. The analysis of covariance (ANCOVA) testing for spatial variation in growth by the initial length as covariant indicated a significant spatial variation in growth rates (Table 1, $p < 0.001$). Turkey's test showed that the growth rates in the western part of Limfjorden were significantly greater than growth rates measured in the eastern part. In addition, growth rates at station K in the eastern area were significantly greater than at other stations in the eastern part.

From November to December, the cages at stations C, D, G and L in the western part of the sound were invaded by starfish *A. rubens* (30–40 mm arm radius). The mean growth of mussels in cages invaded by *A. rubens* was 0.05 ± 0.06 mm (mean ± 2 S.E.), from an initial length of 44 mm. The growth increment corresponded to 0.01 mm week⁻¹. In cages precluding starfish, the mean growth was 0.55 ± 0.15 mm (mean ± 2 S.E.), or 0.14 mm week⁻¹. The analysis of covariance (ANCOVA) testing for spatial variation in growth (excluding cages invaded by starfish) with initial length as covariant indicated a significant spatial variation in growth rates (Table 1, $p < 0.001$). Turkey's test showed that growth rates at stations in the northern areas (subarea 13 and 10) and at station T in the southern broad (subarea 18) were faster than the growth in the central part of the area (subareas 8, 9 and 10).

3.3. Control experiments

Table 1

Results of three separate analyses of covariance (ANCOVA) testing the spatial variability in growth rates estimated by cage experiments

Source	DF	ADJ SS	MS	F	P
<i>January–March</i>					
Covariates	1	0.0059	0.0059	9.18	0.003
Station	13	0.0167	0.0012	1.97	0.027
Error	153	0.1000	0.0006		
Total	167	0.1198			
<i>July–August</i>					
Covariates	1	0.3964	0.3964	64.43	< 0.001
Station	9	0.2392	0.0265	4.32	< 0.001
Error	69	0.4245	0.0061		
Total	79	1.1940			
<i>November–December</i>					
Covariates	1	0.0009	0.0010	0.28	0.597
Station	7	0.2887	0.0413	11.99	< 0.001
Error	87	0.2993	0.0034		
Total	95	0.5883			

The mean length of the shells was used as covariate.

3.3 Control experiments

The growth of mussels in cages was compared to growth of mussels on plates. A two-way analysis of variance of the growth rates in cages and on plates, at the four stations, indicated no significant difference in growth ($p = 0.11$).

3.4. Spatial variability in growth

Growth of mussels from May 1993 to May 1994 in the subareas showed a significant spatial variation (Table 2, $p = 0.011$) and was significantly affected by the initial length of the mussels ($p < 0.001$), but not by their initial biomass ($p = 0.846$). The mean growth rate was 6.3 ± 0.05 mm yr⁻¹ (mean ± 2 S.E.).

In subareas 3 + 5, 4, 10, 11, and 18–19, a significant declining growth rate with increasing shell length was observed (Fig. 4), and growth in each subarea was fitted to the von Bertalanffy equation: $l_t = l_{\infty} - (l_{\infty} - l_0)e^{-Kt}$, where l_0 and l_{∞} are constants representing, respectively, mussel length at time zero and maximum possible length, t is time and K is the growth parameter. The maximum length l_{∞} and the growth parameter K were extrapolated from a Ford–Walford plot of the mean size of the identified cohorts of mussels in 1993 and 1994. The maximum

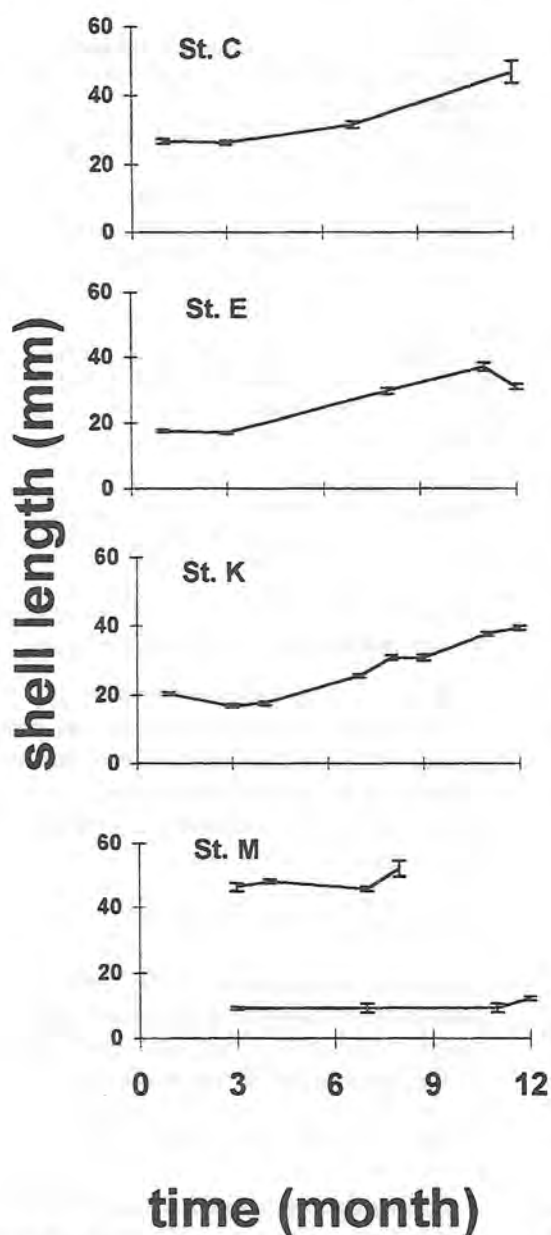


Fig. 3. The change in mean shell length ± 2 S.E. as a function of time of mussels in the natural mussel beds.

length L_{∞} ranged from 5.28 cm in subarea 10 to 6.90 cm in subareas 18–19 (Table 3). The growth parameter K ranged from 0.31 in subarea 11 to 1.42 in

Table 2

Results of an analysis of covariance (ANCOVA) testing the spatial variability in growth rates by the mean length in 1993 and the biomass on each station as covariates

Source	DF	ADJ SS	MS	F	P
Covariates	2	2.927	1.463	16.2	< 0.001
Zone	11	2.455	0.223	2.5	0.011
Error	70	6.337	0.090		
Total	83	11.255			

Covariate	Coefficient	S.D.	t-value	P
Biomass	-0.0013	0.0065	-0.195	0.846
L93	-0.2747	0.0485	-5.655	< 0.001

subarea 3 + 5.

4. Discussion

In the present study, significant differences in growth rates were found when estimating individual growth in cages and from estimates of growth by repeated measurements of mean lengths of discrete size classes on the seabed. While from January to March, a 0.45–3.5 mm reduction in shell lengths was measured in natural mussel beds, caged mussels showed an increase of 0.12 mm over the same period. From July to August, growth in the natural mussel beds ranged from 5.4 to 6.3 mm, significantly faster than the mean growth rates measured for caged mussels (0.13 and 1.98 mm in the period for large and small mussels, respectively). From November to December, no clear tendency in the difference between individually measured caged mussels and the wild stock were observed.

Growth of mussels was in the study measured by two different methods. Four stations were sampled bimonthly by one of two different dredges, and the growth of discrete size classes measured. In January and April, the seabeds was sampled by a model of a commercial mussel dredge, and the rest of the samples were collected by a smaller triangular dredge. Preliminary investigations have demonstrated that the mussel dredge normally samples mussels unbiased, but size selection is observed when dredging at

Table 3

Limfjorden
The maximum shell length l_{∞} and the growth parameter K for subareas in Limfjorden in 1993–1994 estimated from the Bertalanffy growth equation

Subarea	Numbers of stations	l_{∞}	K
3+5	15	6.32	1.42
4	8	6.73	0.33
10	10	5.28	0.45
11	12	5.49	0.31
18–19	18	6.90	0.46

Data from subareas 3 and 5, and 18 and 19 are pooled.

beds formed by mussels weakly attached to the

substratum and to other conspecific mussels. At three stations, an initial reduction in shell length was observed coinciding with the use of two different dredges in January and March. At station K, a reduction in mussel mean length was observed from January to April, indicating that the initial decrease in shell length at station C, E, and K is not an artefact of the choice of dredge.

Growth of individual marked mussels in cages was measured at 16 stations. Fouling of cages was observed only in July–August, when ascideans settled on the cages in the western part of the sound. The reduced flow of water and suspended food

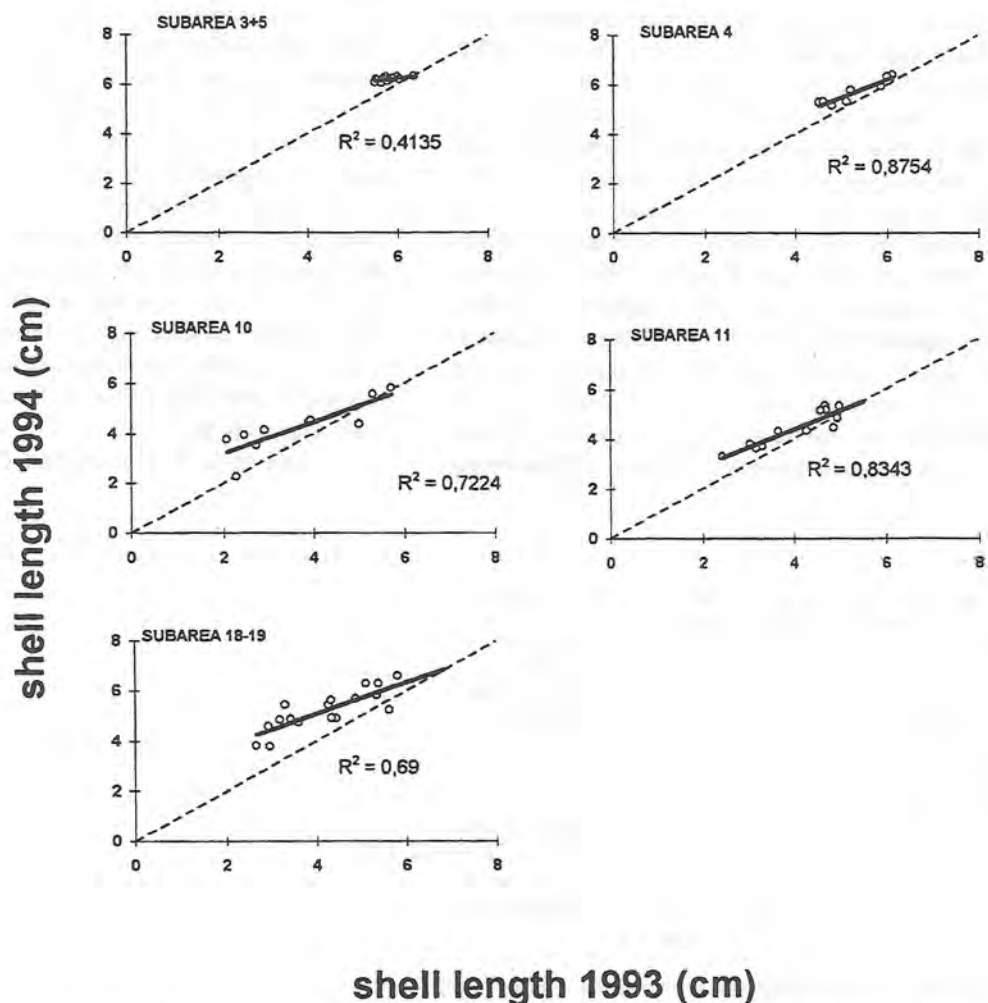


Fig. 4. Ford-Walford plots of mean shell length of mussel cohorts, 1993 and 1994, for different areas of Limfjorden.

Limfjorden

particles through the cages may result in a reduced growth rate. Anyway, the growth rates measured in the western part were significantly greater than the growth rates in the eastern part of the sound.

The initial density of mussels in the four sampled seabeds was 2.2 kg m^{-2} , much larger than the biomass in the cages. The growth rate of mussels is reported to be density-dependent (Fréchette and Bourget, 1985a,b; Asmus and Asmus, 1991), and a reduced growth rate in the seabed could be explained by this intraspecific competition. In July to August, the opposite situation was observed, indicating that other mechanisms control the change in the mean length of the mussel population. The density of mussels and the topography of the mussel bed interact with the dynamics of the mussel populations. Mussels living near the edge of beds are observed to be larger than mussels in the centre (Newell, 1990; Svane and Ompi, 1993). Likewise, in dense mussel beds, a vertical size difference between mussels in the upper layer of the bed supplied constantly with food and oxygen and water, and those living in the interior of the bed, can be expected as a result of differential growth, mortality or recruitment (Kautsky, 1982; Alvarado and Castilla, 1996). Jørgensen (1980) measured oxygen concentration in bottom waters in Limfjorden and observed reduced concentrations above mussel beds. The degree of oxygen depletion increased with size and density of the mussel beds. In situations with low oxygen concentrations, a frequent summer condition in Limfjorden

small mussels in the interior of the beds may show the highest mortality resulting in an overall increase in mean shell length as a result of size-specific mortality.

Worrall and Widdows (1984) investigated the seasonal variation in mortality of *M. edulis* in River Lynher in Southwest England. Minimum mortalities were observed in winter; maximum mortalities in April coincided with mussel spawning. Greatest mortalities were estimated in the larger size classes. In 1995, *M. edulis* spawned from mid-April to late May in Limfjorden (Moser, pers. comm.), so post-spawning mortality cannot explain the observed reduction in the mean length in January to March.

At stations C and E in the western part of Limfjorden in January, there were dense populations of *A. rubens*, an important predator of *M. edulis* (Dare, 1982). The feeding rate of starfish is temperature-dependent; they are reported to feed at a maximum rate between 10–13°C, and continue feeding in winter until February. In summer, the feeding activity decreases as temperatures rise to 16–18°C (Hancock, 1955, 1958). Preliminary diver observations indicated that *A. rubens* feeds on the largest mussels in the beds. Size-specific predation on the larger, slow-growing mussels in winter results in a reduction in shell length, as observed in January to March. At station E, a reduction in mussel mean size was also observed from November to December, coinciding with mussel fishery.

Growth rates were estimated by the Bertalanffy

Table 4
The maximum shell length L_{∞} and the growth parameter K estimated for different mussel populations

Location	L_{∞}	K	Author
Limfjorden, DK	52.8–69.0	0.31–1.42	Present study
Mariager Fjord, DK	80.8–86.3	0.35–0.45	Theisen, 1975
Genner Fjord, DK	80.2–108.2	0.14–0.26	—
Randers Fjord, DK	50.7–54.5	0.24–0.31	—
Kolding Fjord, DK	77.2–88.7	0.17–0.16	—
Wadden Sea	77.6	0.56	Theisen, 1968
Plymouth, UK	81.3–93.8	0.22–0.24	Bayne and Worrall, 1980
Askö, Baltic Sea	32	0.12	Kautsky, 1982
Disko, Greenland	77.5–283.9	0.022–0.162	Theisen, 1973
Thule, Greenland	94.5–153.3	0.048–0.053	—

The data for Askö in the Baltic Sea was extrapolated from a figure in the paper.

Limfjorden equation for five subareas in *Limfjorden* for 1993–1994, and were high compared to other areas (Table 4). The study showed faster growth in the western part of the fjord in subareas 3 and 5. In situ observations were supported by results of cage experiments in July and August 1995. In *Limfjorden*, a net west-east flow results in higher salinity in the western part. The annual salinity range in the western part in 1982–1993 was 29–32‰, and 25–28‰ in the central part. In the southern part of the area, the salinity ranged between 22 and 25‰ (data from the counties surrounding *Limfjorden*). In a reciprocal transplantation experiment, Kautsky et al. (1990) showed that blue mussels grow faster in higher salinities.

Subareas 3, 5, and 6 constitute a strait connecting the western parts (subareas 1–2) and the central parts of the sound (subareas 7–11). In the narrow strait, the current speed and mixing rate of the bottom and top layer of the water column are increased. The growth of *M. edulis* is affected by the concentration, and transport of food. Fréchette and Bourget (1985a,b) demonstrated that growth of blue mussels was depressed close to the bottom because of depletion of food in the benthic boundary layer, and that turbulence was an important transport mechanism of seston to the bottom layer. In summer periods with calm weather, a temperature stratification of the water column is observed in *Limfjorden* (Jørgensen, 1980). The stratification results in a reduction of the transport of phytoplankton from the highly productive surface layers downward to benthic suspension feeders (Møhlenberg, 1995).

Composition and concentration of seston both affect growth of mussels (Bayne et al., 1989; Smaal and van Stralen, 1990). Data from the counties surrounding *Limfjorden* indicate that primary production is greatest in the southern part of the sound (subarea 19) ranging from 1200 to 4000 mg C m⁻² day⁻¹ in summer. In the central and the western parts of the sound, primary production ranges from 500 to 2400 mg C m⁻² day⁻¹ in summer. The concentration of Chl. a. range from 20 µg l⁻¹ in the southern areas to 6–7 µg l⁻¹ in the central and western parts of the area. The results of this study showed that the growth of mussels was faster in the western part of the area, not correlated to the amount of food. Moreover, investigations in subarea 8–10 in summer 1994 and 1995 indicated that the mussels were not food-limited

(Møhlenberg, pers. comm.)

The standing stock of mussels available for the fishery is determined by the production of mussels and also by natural mortality. The fastest growth rate was measured in the western part of the sound, an area with a high density of starfish. Kristensen and Lassen (1997) showed that growth rate of relayed mussels was larger in the western subareas than in the central subareas. Fifty-one vessels have licenses for mussel dredging in *Limfjorden*. All operate in the same two or three areas, at the same time, depleting the local mussel stocks before moving to another area. The populations are re-established following new recruitment. The annual growth increment of mussels with an initial length of 20 mm was about 20 mm yr⁻¹. Assuming that these 20 mm mussels settle in spring, the minimum period from recruitment to harvesting (length = 45 mm) is 2.5 yr, for fast-growing mussels.

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Søstjerner, *Asterias rubens* på muslingebanke

The interactions between bed structure of *Mytilus edulis* L. and the predator *Asterias rubens* L.

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Abstract

The feeding behaviour of asteroids is usually analyzed with optimal foraging models, which assume that asteroids maximize the ratio of energy uptake relative to energy used in the feeding process. The behaviour of *Asterias rubens* feeding at subtidal beds of *Mytilus edulis* was studied in order to evaluate effects of mussel bed structure on predation rate and size selection of prey. Field observations showed that *Asterias* feeds on mussels whose size ~~is~~ ^{are} the same or larger than the mean size for the population. The solid structure of interconnected mussels forming the bed restricts *Asterias* predation to only those mussels situated at the bed surface. A field experiment demonstrated that *Asterias* consumption rate of mussels was higher at beds with an intact structure of mussels compared to beds where the bands interconnecting the mussels were broken and mussel orientations changed. A laboratory experiment revealed that attachment of mussels did not affect starfish predation rates and indicated that change in orientation of mussels may reduce predation rates. In field and laboratory experiments, increased attachment of mussels was observed when exposed to *Asterias*. The study demonstrated that the feeding behaviour of *Asterias* is restricted by the complex structure of interconnected mussels in beds, which has to be integrated in optimal foraging models. © 1998 Elsevier Science B.V.

Keywords: *Mytilus edulis*; *Asterias rubens*; Optimal foraging; Mussel bed structure

1. Introduction

Field experiments on hard bottom substrata have identified starfish as important structural component of lower shore and sublittoral ecosystems (Paine, 1966, 1974; Menge et al., 1994; Navarette and Menge, 1996). Paine (1966) demonstrated that *Pisaster ochraceus* reduced the density of the competitively dominant *Mytilus californianus* increasing the diversity of competitive weaker species. Menge et al. (1994) observed spatial variation in predation intensity of *P. ochraceus* feeding on *M.*

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californianus and *Mytilus trossulus*. The variation depends of wave exposure and recruitment and growth of prey. Mussels are reported to vary in accessibility to predating starfish. Paine et al. (1985) demonstrated that larger individuals of *M. californianus* and *Perna canaliculus* coexisted for years with the predators *P. ochraceus* and *Stichaster australis*, respectively; whereas all size classes of *Perumytilus purpuratus* were vulnerable to predation from *Heliaster helianthus*, and no size refuge was reached. Starfish is also reported to structure sublittoral soft bottom ecosystems. The blue mussel, *Mytilus edulis*, is an important prey species for *Asterias rubens*, and the starfish has been reported to aggregate seasonally at beds of mussels totally destroying local mussel populations (Spärck, 1932; Rasmussen, 1973; Sloan and Aldridge, 1981; Dare, 1982; Kristensen and Lassen, 1997). o c d

In order to explain the interaction between predating starfish and prey, the mussels/ optimal foraging model is introduced. A prerequisite for applying optimal foraging models to asteroids is an understanding of feeding behaviour parameters, such as prey size (Paine, 1976; O'Neill et al., 1983; Penney and Griffiths, 1984; McClintock and Robnett, 1986) and force used to open shells (Hancock, 1974; Norberg and Tedengren, 1995). According to these models, asteroids are expected to feed on prey maximizing energetic return in relation to energy used in the feeding process. Feeding trials, in which asteroids are offered mussel prey in laboratory experiments are a commonly used method for analyzing feeding behaviour (O'Neill et al., 1983; McClintock and Robnett, 1986). However, most experiments to date have excluded prey characteristics, such as the structure of mussel beds or patches, and the effects of mussel attachment to the substratum. u u

Mussels in dense patches form tri/dimensional matrices. Kautsky (1982) showed that *M. edulis* form beds with the fast-growing large-size fraction in the top layer and the smaller mussels in the bottom layer. This bimodal distribution is also reported for *P. purpuratus* in Chile (Alvarado and Castilla, 1996). In addition, mussels close to the edge of the beds are larger than mussels in the center of the beds (Newell, 1990; Svane and Ompi, 1993). Differences in size distribution are hypothesized to be caused by differentiated recruitment, predation or growth caused by food depletion and movement (Kautsky, 1982; Alvarado and Castilla, 1996). u

The mussel beds are composed primarily of three components: the tri/dimensional matrix of interconnected dead or alive mussels, the organo-rich bottom layer, and the associated flora and fauna (Seed and Suchanek, 1992). The formation of byssus threads is important for the structure of mussel beds. The properties and functions of byssus threads are described by Smeathers and Vincent (1979) and Waite (1983). u

Dayton (1971) concluded that survival of large intertidal mussels (*M. californianus*) in dense intertidal mussel beds at San Juan Island, Washington, is dependent on its spatial continuity, and if the continuity is broken, wave action dislodges the remaining mussels from the substrata. Witman and Suchanek (1984) showed that more force is required to dislodge mussels from the edge of a mussel bed than from the center of a mussel bed. This observation can be explained by the tendency of mussels to form multilayered beds. Mussels at the edge form a strong attachment to the primary substratum, whereas mussels in center form a weaker attachment to adjacent mussels. Alternatively, mussels at the edge are more affected by flow and are induced to form a stronger attachment.

Martella (1974) observed, in a laboratory study, that *M. edulis* produce more byssus threads when kept in clumps than individually kept mussels. This observation was explained by a tactile stimulation when the foot was in contact with other mussels.

The object of this study was to analyze the effect of mussel bed structure on susceptibility of mussels to predation by *Asterias*. In the field, the size of preferred mussels were measured and compared to the mean size of the population. In field and laboratory experiments, the predation rate was estimated as a function of the structure of mussel beds and byssus attachment of mussels.

2. Methods

The study was conducted in Limfjorden, Denmark (Fig. 1), a 1575-km² sheltered inlet open to the North Sea in the west and to Kattegat in the east. The salinity ranges from 32‰ in the western part to 24‰ in the eastern part of the inlet. In Limfjorden, an important fishery on natural stocks of blue mussels, *M. edulis*, takes place, with annual landings exceeding 100 000 tonnes. The inlet has a high nutrient load, and it receives nutrients from the surrounding areas. As a result, primary production is relatively high, and often exceeds 1000 mg C m⁻² day⁻¹ in summer in most parts of the inlet (County of Viborg).

2.1. Field observations of sizes of mussel prey

The relation between size of *Asterias* and size of mussels predated by *Asterias* was analyzed in July and November 1995 and May 1996. *Asterias* that were actively preying on mussels were collected using SCUBA ($n = 11–32$) at six stations (Fig. 1) at 7–9 m depth. The criteria for designating an *Asterias* as exhibiting feeding behaviour was that the starfish was attached to a single mussel with its stomach extruded. The arm radius of the starfish and shell length of the captured mussels ~~was~~ were measured. In addition, the size distribution of the blue mussel population was described from samples taken by a triangular dredge on each station.

2.2. Field observations of mussel attachment

Attachment of *Mytilus* was measured at four stations in May 1996 (Fig. 1). A SCUBA-diver placed an alligator clip connected to a spring balance on single mussels and the attachment force, ~~was~~ was measured as the maximum weight when detaching the mussels ($n = 11–33$). Afterwards, the shell lengths of the mussels were measured. The densities of *Asterias* were estimated by frame sampling. A diver randomly placed a ring (diameter, 60 cm) on the bottom and counted the numbers of *Asterias*. Thirty samples were taken at two stations, with a low starfish density, and 12 samples at the station with the highest density. Finally, starfish abundance at the station with the lowest density was 0.1 individual m⁻² (visual observation).

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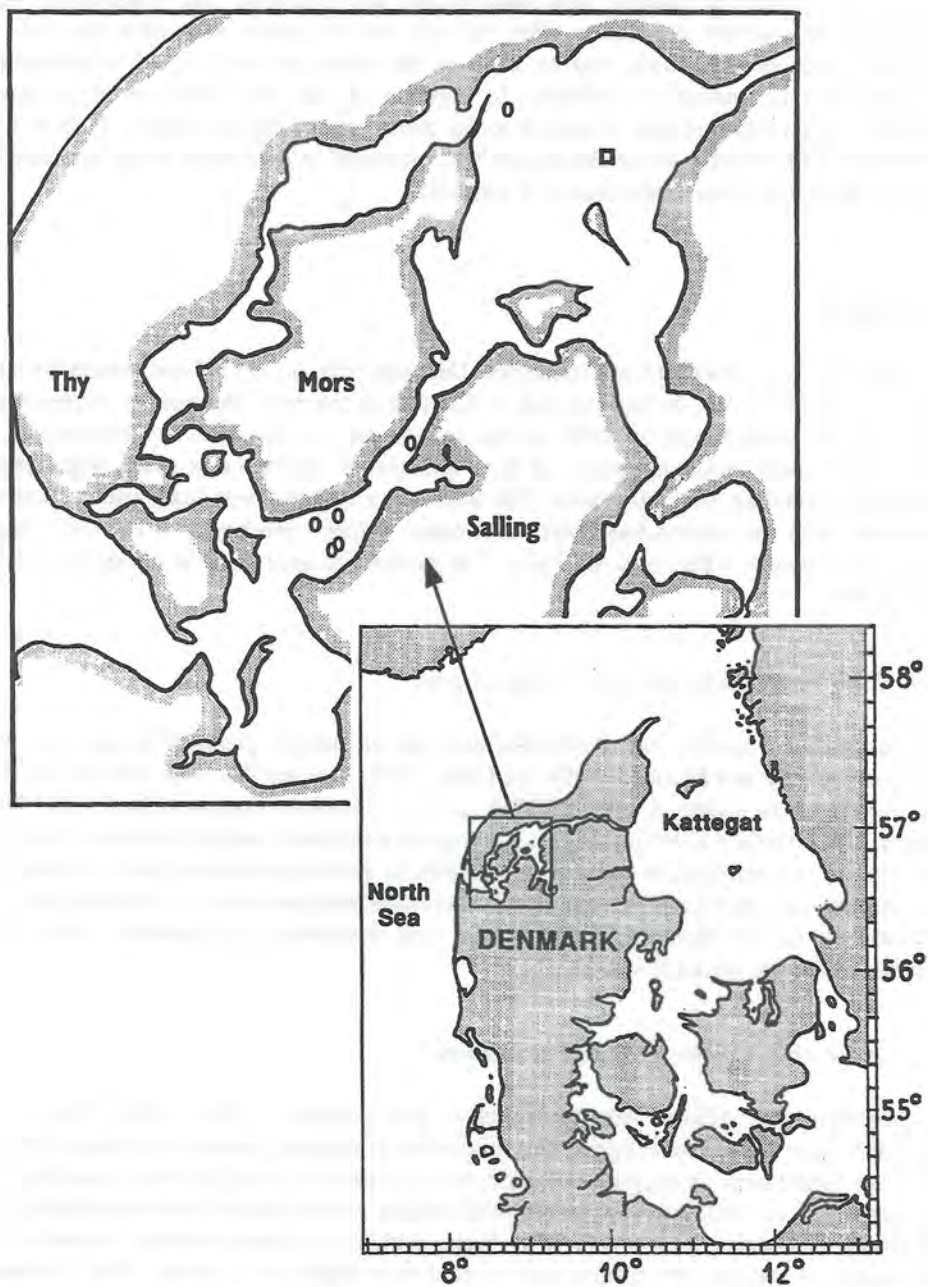


Fig. 1. Map of Limfjorden, Denmark showing the sampling sites of feeding *Asterias rubens* (○), and the location of the field experiment (□).

2.3. Field experiment: predation rate as a function of mussel bed structure

A field experiment was conducted in May 1996 in the central part of the inlet (Fig. 1) at 8 m depth to investigate the effect of the structure of mussel beds on the predation rate of *Asterias*. No *Asterias* were observed at this site before the experiment. The biomass (± 2 S.E.) of mussels in the beds was $5.0 \pm 0.9 \text{ kg m}^{-2}$, and the shell length (± 2 S.E.) was 39 ± 1 mm. Twelve cages ($L/35$ cm; $W/75$ cm; $H/35$ cm; mesh size/1 cm) were positioned over a mussel bed. Four cages served as controls with no *Asterias* added and mussels untouched. Ten *Asterias* with an arm radius (± 2 S.E.) of 73 ± 2 mm were placed in each of the remaining cages. In four of these cages, the structure of the mussel bed was broken before the addition of *Asterias* by mixing the mussels and breaking interconnecting byssus threads. In the last four cages *Asterias* was added to an intact mussel bed.

After 11 days exposure, *Asterias* were removed from the cages and valves of dead mussels collected. Only empty shells with an unbroken hinge ligament were recorded as newly predated. Empty shell abundance and shell lengths were recorded. Afterwards, the surviving mussels were collected as coherent clumps and the attachment force of single mussels to the clumps was measured in the laboratory for 10 mussels from each cage.

2.4. Laboratory experiment: predation rate as a function of mussel attachment

An aquaria experiment, parallel to the field experiment, was conducted at Rønbjerg Marine Biological Laboratory in May 1996. The feeding rate of *Asterias*, feeding on *Mytilus*, was investigated as a function of attachment. The experiment was performed in two identical blocks. In each block, each of 15 aquaria ($L/50$ cm; $W/18$ cm; $H/25$ cm) were seeded with 43 mussels with a shell length (± 2 S.E.) of 39.1 ± 0.3 mm. The mussels were placed on plates of slate in running seawater and allowed to attach. After 24 h, all mussels in five of the aquaria were detached and replaced on the plates. Eight *Asterias* with an arm radius (± 2 S.E.) of 75 ± 1 mm were placed in each of the five aquaria with disturbed structure, and in five aquaria with intact clumps. The last five aquaria served as controls without addition of *Asterias*. After 5 days of exposure the numbers of dead mussels were counted and shell lengths measured. Afterwards the plates of slate were removed from the aquaria, and the attachment force of six mussels in each aquaria were measured as previously described. The size distribution of the surviving mussels was recorded.

2.5. Data analysis

Numbers of dead mussels as a function of bed structure from the field and laboratory experiments were analyzed using one-way ANOVA. Experimental runs were used as blocks in the analysis of the laboratory experiment. The attachment force were analyzed in a nested two-way ANOVA with cage/aquaria nested to addition of *Asterias*. Tests were followed by the Tukey multiple comparison procedure.

It was also tested, whether the predation rates measured for mussels in intact beds was

correlated to the attachment force of the mussels in both the field and laboratory experiments.

A ratio was calculated which compared the shell length of predated mussels to the size distribution of the remaining live mussels measured in the laboratory experiments. The ratio obtained from aquaria with an initially destroyed structure was compared to the ratio obtained from aquaria with intact structure using a one-way ANOVA.

Before the ANOVA, data were tested by F_{\max} -tests to ensure homoscedasticity.

3. Results

3.1. Field observations of sizes of mussel prey

The relationships between size of predated *Mytilus* compared to (a) the size distribution of the total mussel population, and (b) to the size of mussels and size of the corresponding predating *Asterias* were analyzed for six stations. The mean size of *Asterias* ranged from 57 to 116 mm, and the size of predated mussels ranged from 14 to 59 mm, with means from 34.1 to 48.4 mm (Table 1). At stations with two discrete size classes of mussels, the smaller size class was significantly smaller than the mean size of the predated mussels (Table 1, $P = 0.00$). At two stations, the size of predated mussels was significantly larger than the large size class of mussels ($P = 0.02$), and at two other stations the size of predated mussels was significantly smaller than that for the total population ($P = 0.00$ – 0.04).

A significant correlation ($P = 0.03$) was observed between size of *Asterias* and size of predated mussels only at the station with largest variation in sizes of *Asterias* (Table 1).

Table 1
Shell lengths of *Mytilus* populations (size class 1 + 2), predated mussels and the corresponding predating *Asterias* at five different stations.

Shell length (mm)								Arm (mm), <i>Asterias</i> radius		Corr. $ r_p $
Predated mussels		Size class 1		Size class 2						
Mean	2 S.E.	Mean	2 S.E.	p_1	Mean	2 S.E.	p_2	Mean	2 S.E.	\wedge
48.4	2.1	9.2	1.4	0.00	45.6	0.6	0.02	57.0	5.0	0.09
34.1	2.0	—	—	—	37.0	1.3	0.20	102.2	6.3	0.26
38.3	3.8	—	—	—	42.6	1.2	0.04	104.7	5.7	0.32
44.5	2.9	16.1	2.8	0.00	45.4	0.9	0.51	100.0	8.4	0.11
36.0	1.5	—	—	—	39.6	0.7	0.00	116.1	9.4	0.03
42.6	2.3	—	—	—	40.2	0.9	0.02	92.1	5.0	0.37

Difference in mean size comparing predated mussels and the cohorts of mussels were tested by use of a t -test. p_1 and p_2 indicate the significance of the tests. The relations between the size of the mussels and the predating *Asterias* were tested by an analysis of correlation. p_3 indicates the significance of the correlation. Bold type indicates conventional statistical significance at $P < 0.05$.

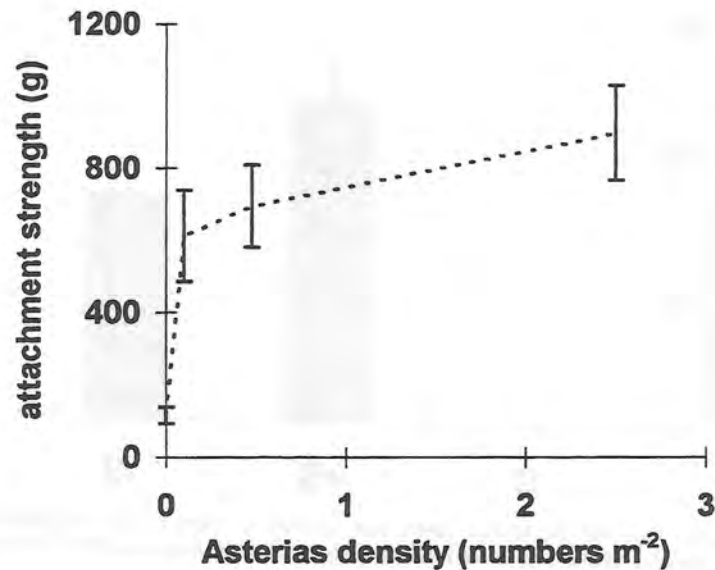


Fig. 2. Field measurements of the attachment strength (mean ± 2 S.E.) of *Mytilus edulis* as a function of density of *Asterias rubens*.

3.2. Field observations of mussel attachment

Attachment of *Mytilus* was measured at four stations. The detachment force increased with density of *Asterias* ranging from 115 g at the station without *Asterias* to 900 g at the station with 2.5 *Asterias* m⁻² (Fig. 2).

3.3. Field experiment: predation rate as a function of mussel bed structure

The cage experiment involving the effect of the structure of the mussel bed on predation rates by *Asterias*, showed a significant effect of initial breakage of bed structure (Table 2, $P = 0.008$). In cages with intact structure 47 ± 7 mussels cage⁻¹ (mean ± 2 S.E.) were dead, and in cages with broken structure 33 ± 5 mussels cage⁻¹

Table 2

Field experiment: one-way ANOVA of the number of dead mussels, *Mytilus edulis*, in a undisturbed and a disturbed mussel bed added *Asterias rubens*.

Source	DF	SS	MS	F	P
treatment	1	406	406	15.0	0.008
Error	6	163	27		
Total	7	569			

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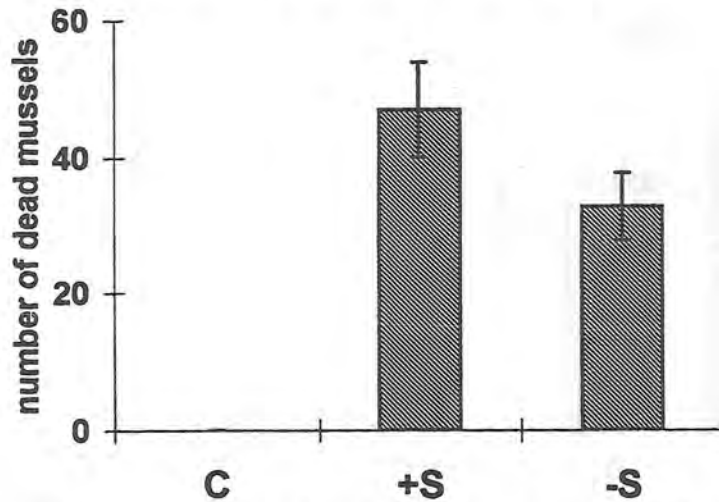


Fig. 3. Number of dead mussels, *Mytilus edulis*, after 11 days in cages in the field exposed to: + S/undisturbed bed, *Asterias* added; - S/initial breakage of byssus threads, *Asterias* added; C/undisturbed bed, no *Asterias* added.

were dead (Fig. 3). No dead mussels were observed in the control cages. The shells of ingested mussels were not attached to other mussels or to the substratum. No significant difference was observed in size of predated mussels in cages with broken structure compared to cages with intact structure (one-way ANOVA, $P = 0.16$).

The attachment strength of mussels in the cages was significantly affected by the presence of *Asterias* (Table 3, $P = 0.001$). Mussels in cages with *Asterias* were significantly more strongly attached to the mussel bed compared to those in control cages without *Asterias* ($P < 0.05$) (Fig. 4).

The correlation analysis of the relation between *Asterias* predation rates and the attachment force of the mussels in the cages with intact structure indicated no correlation ($R^2 = 0.28$, $P = 0.47$), indicating that the starfish do not prefer to feed on the more loosely attached mussels.

Table 3

Field experiment: nested two-way ANOVA testing the effects of addition of *Asterias rubens* on byssal attachment of *Mytilus edulis* in cages over undisturbed beds.

Source	DF	SS	MS	F	P
<i>Asterias</i>	1	171 125	171 125	12.20	0.001
Cage (<i>Asterias</i>)	6	145 870	24 312	1.73	0.125
Error	72	1 009 600	14 022		
	79	1 326 595			

The experiment was conducted in 12 cages and the measurements of attachment in each cage were nested to the treatments.

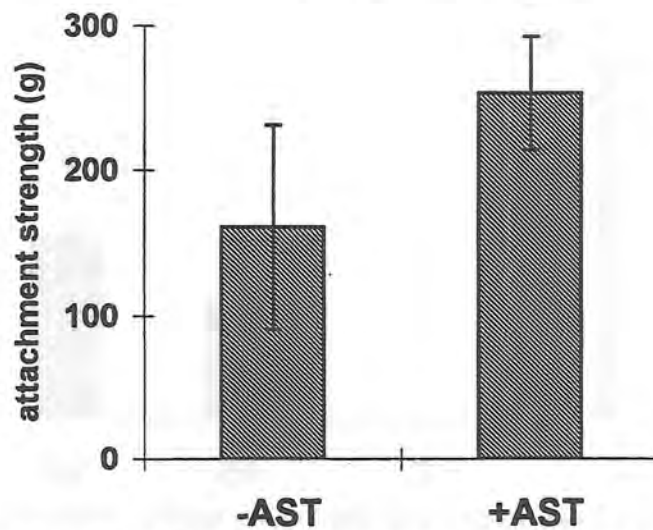


Fig. 4. Attachment strength (mean ± 2 S.E.) of *Mytilus edulis* as a function of the presence (+AST) or absence (-AST) of *Asterias rubens* in cages with intact bed structure.

3.4. Laboratory experiment: predation rate as a function of mussel attachment

The experiment designed to test the effect of initial breakage of the established bed structure, in relation to intact structure on the predation rate of *Asterias*, showed no significant effect (Table 4, $P = 0.242$). In cages with intact structure 4.8 ± 2.6 mussels cage^{-1} (mean ± 2 S.E.) were dead compared to 7.2 ± 3.3 mussels cage^{-1} in cages with broken structure (Fig. 5). No dead mussels were observed in the control aquaria. No significant difference was observed in size of predated mussels in cages with broken compared to intact structure (one-way ANOVA, $P = 0.72$).

Addition of *Asterias* to mussels established on the plates of slate significantly affected the attachment strength (Table 5, $P = 0.000$). Fig. 6 shows that mussels exposed to *Asterias* were attached significantly more strongly than mussels in the control aquaria.

The correlation analysis of the relation between *Asterias* predation rates and the

Table 4

Laboratory experiment: two-way ANOVA of the number of dead mussels, *Mytilus edulis*, in a undisturbed and a disturbed mussel bed added *Asterias rubens*.

Source	DF	SS	MS	F	P
Run	1	24.20	24.20	1.24	0.282
Treatment	1	28.80	28.80	1.47	0.242
Error	17	333.00	19.59		
Total	19	386.00			

The experiment were conducted in two parts, and the two runs constitute the second factor in the analysis.

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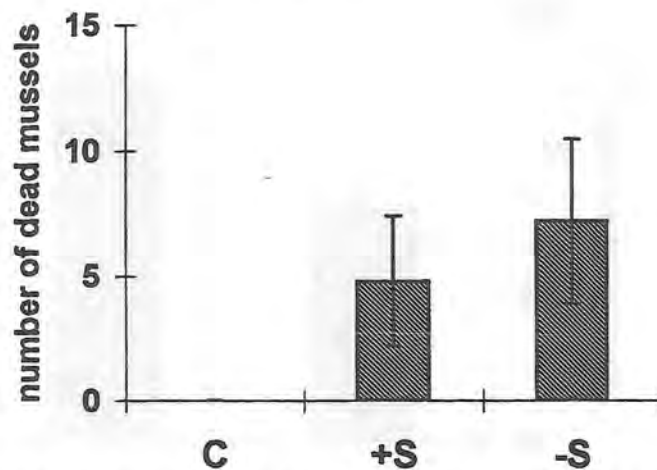


Fig. 5. Number of dead mussels, *Mytilus edulis*, after 5 days in aquaria in the laboratory exposed to: +S/undisturbed bed, *Asterias* added; -S/initial breakage of byssus threads, *Asterias* added; C/undisturbed bed, no *Asterias* added.

attachment force of the mussels in the aquaria with undisturbed mussels indicated no correlation ($R^2 = 0.024$, $P = 0.67$), indicating that the starfish did not prefer to feed on the most loosely attached mussels.

The ratio between the size of predated mussels (+P) and surviving mussels (-P) is shown in Fig. 7 for mussels in aquaria with intact structure and aquaria with broken structure. No significant difference was observed in the ratio (one-way ANOVA, $P = 0.066$), but a trend indicates that mussels eaten in aquaria with intact structure were larger than mussels eaten in aquaria with broken structure.

4. Discussion

Investigations of size-selective predation on mussels by asteroids are often conducted in the laboratory, neglecting the importance of the structure of mussel beds. Investigations conducted in the laboratory and in the field indicate that asteroids feed on mussels of intermediate size (Paine, 1976; McClintock and Robnett, 1986). O'Neill et al. (1983) showed in a laboratory experiment that *A. vulgaris* fed on the small-size fractions

Table 5

Laboratory experiment: nested two-way ANOVA testing the effects of addition of *Asterias rubens* on byssal attachment of *Mytilus edulis* attached to plates in aquaria.

Source	DF	SS	MS	F	P
<i>Asterias</i>	1	253 920	253 920	20.46	0.000
Aquaria (<i>Asterias</i>)	8	69 193	8649	0.70	0.694
Error	110	1 365 433	12 413		
Total	119	1 688 547			

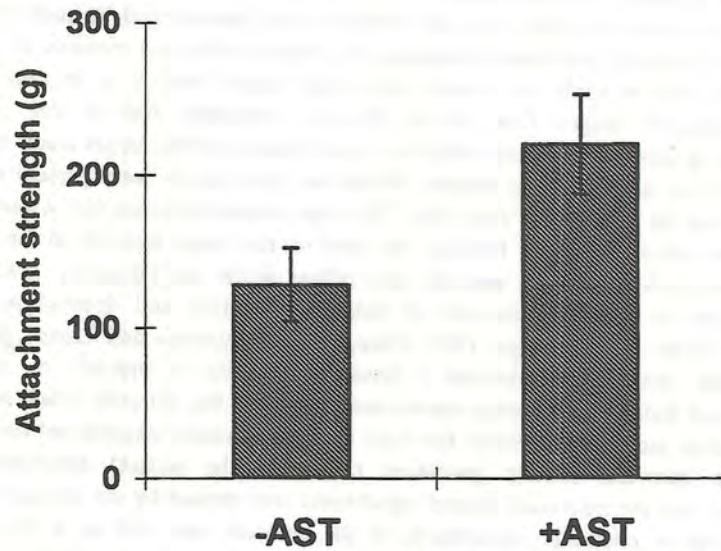


Fig. 6. Measurements of the attachment strength (mean ± 2 S.E.) of *Mytilus edulis* on plates of slate in aquaria as a function of the presence (+ AST) or absence (–AST) *Asterias rubens*.

of *M. edulis*. Penney and Griffiths (1984) measured starfish size selection and consumption rate of mussels, and formulated a model showing that asteroids feeds on mussels of intermediate size when one cohort is present, and on small mussels when two

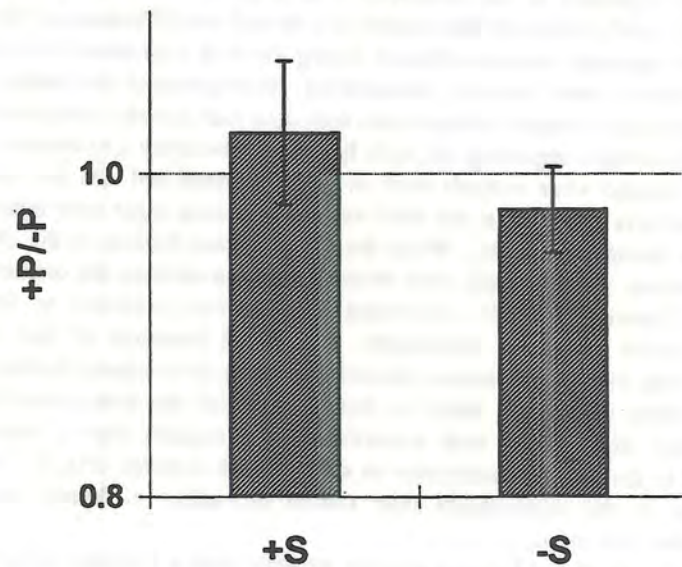


Fig. 7. The relation between the shell length of predated mussels and surviving mussels (mean ± 2 S.E.) in the laboratory experiment in aquaria with undisturbed mussel structure (+ S) and in aquaria with an initial disturbance of the mussel structure (–S).

cohorts are present. The only study, which includes mussel attachment as an important parameter for predation rate, was performed by McClintock and Robnett (1986). They showed that asteroids maximize foraging gain when feeding on mussels of intermediate size. In the present study the mussel mean size ranged from 9 to 46 mm; the size of predated mussels ranged from 14 to 59 mm, indicating that all size classes were susceptible to predation. No size selection was observed of the larger fraction of mussels when only one size class was present. When two size classes were present no predation was observed on the smaller size class. The observations indicate that *Asterias* show no mussel size selectivity when feeding, but feed on the larger mussels in the top layer of the bed, whereas the smaller mussels take refuge in the bed (Kautsky, 1982). They are first exposed to predation in case of massive predation and destruction of the bed structure (Sloan and Aldridge, 1981; Dare, 1982; Kristensen and Lassen, ~~in press~~). 2 1997

The field observations showed a firmer attachment of mussels on stations with *Asterias*, and field and laboratory experiments revealed that mussels attach more strongly when starfish are present. Either the field or the laboratory experiment demonstrated a correlation between starfish predation rates and the mussel attachment strength, suggesting that the increased mussel attachment was caused by the presence of *Asterias* by a tactile or chemical stimulation of the mussels, and not as a result of higher predation rates on loosely attached mussels. Dolmer and Svane (1994) reported that when mussels are held in turbulent water, 81% of the potential strength of attachment is actually used for attachment. To the contrary, when held in still water, only 21% of the potential strength is used for attachment, indicating that the organisation of byssus threads is influenced by flow velocity. The strength of byssal attachment is also reported to be affected by season (Price, 1980), size of mussel (Lee et al., 1990), salinity, temperature, exposure to air, chemicals (van Winkle, 1970), substratum type (Young, 1983, 1985), and location of the mussel in a mussel bed (Witman and Suchanek, 1984).

Shells of ingested mussels collected during the field experiment were not attached to the substratum or other mussels. Furthermore, observations of the feeding mechanism of *Asterias* preying on natural mussel beds indicated that *Asterias* detaches the majority of mussel prey before ingestion. In both field and laboratory experiments, feeding rates were not reduced when mussels were in an undisturbed bed. On the contrary, a higher feeding rate was measured in the field experiment using cages over intact bed structure, and thus a harder attachment. When the structure was broken in the cages, the byssal interconnection of the mussels were destroyed, but in addition the orientation of mussels changed. Christensen (1957) described that *Asterias* preferred to feed on mussels orientated with the hinge downwards. The initial breakage of bed structure forced mussels away from this position, probably resulting in a reduced feeding rate. The field and laboratory experiment failed to demonstrate that the byssus attachment acts as an anti-predator defence. In both experiments the mussels had a reduced attachment compared to the field measurements on stations with *Asterias* (Fig. 2). The loose mussel attachment in the experiments may reduce the effect of byssus attachment as an anti-predator preventor.

The predators of bed-forming mussels struggle with a complex tri-dimensional matrix of interconnected animals, often with a vertical and horizontal bimodal size distribution (Kautsky, 1982; Newell, 1990; Svane and Ompi, 1993; Alvarado and Castilla, 1996). 2

The structure of the beds is reported to provide refuge for smaller mussels potentially exposed for predation (Bertness and Grosholz, 1985). The presence of associated fauna is reported to reduce asteroid predation of mussels (Kaplan, 1984). This study demonstrated that the structure of the mussel bed restrict *Asterias* when feeding on mussels. The use of optimal foraging models analyzing feeding behaviour may necessarily incorporate parameters describing the structure of mussel beds and availability of different size classes of mussels. The optimal foraging model for asteroids feeding on mussels structured in beds not only have to incorporate the size selection and the force used to open the mussels, but also have to describe the energy cost of bringing the mussels in the right position for an asteroid attack.

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Dolmer, P.; P. S. Kristensen og E. Hoffmann. Dredging of blue mussels (*Mytilus edulis* L.) in a Danish sound: estimation of stock sizes and fishery-effects on mussel population dynamic. - Submitted til Fisheries Research.



Filtrerende blåmuslinger

Dredging of blue mussels (*Mytilus edulis* L.) in a Danish sound: estimation of stock sizes and fishery-effects on mussel population dynamic.

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Abstract - In April 1993, 1994 and 1995 the abundance of blue mussels, *Mytilus edulis* L., was estimated in Limfjorden, Denmark. The stocks were assessed by using a 1:2 scaled model of a commercial mussel dredge. The efficiency of the mussel dredge was analysed by comparing dredge samples with those samples collected by diver. Dredge efficiency increased with increasing biomass of mussels. Mean efficiency was estimated at 17%. The fishing area in Limfjorden (700 km²) is divided into 22 fishery zones and mussel stock sizes were calculated for each zone. From April 1993 to April 1994 the total stock size declined from 771 000 to 616 000 tons. In the same period the exploitation rate in the fishery was 14 % of the 1993 stock, and significantly correlated with the change in stock. In April 1995 the total mussel stock was reduced to 494 000 tons. The mean exploitation rate in 1994-1995 was 15%. No correlation was observed between the change in the mussel biomass and the exploitation rate. In summer 1994 a long period of oxygen depletion was observed in parts of Limfjorden. This caused a mass mortality of 33 % of the mussels in the affected areas. In fishery zones without oxygen depletion a 46 % increase in the mussel stocks was estimated. The massive loss of blue mussels caused by oxygen depletion exceeds the annual landings of mussels from the fishery.

Key words: blue mussel, *Mytilus edulis*, biomass, effects of fishery, effects of oxygen depletion, stock size, dredge efficiency.

Introduction

In Limfjorden, Denmark (Fig. 1) an extensive fishery of blue mussel (*Mytilus edulis* L.) takes place. Limfjorden is a 1 575 km² shallow water sound open to the North Sea to the west and to Kattegat in east. Salinity ranges from 24 to 32 ppm and the area is highly eutrophic caused by nutrient rich runoff from a 7 500 km² watershed. A large primary production sustains a high growth rate of blue mussels compared to north European fjords and estuaries (see Dolmer, in press). In the enclosed parts of Limfjorden the water column is often stratified during summer resulting in stagnant bottom water for up to several weeks. This situation frequently results in oxygen depletion and subsequently mass mortality of blue mussels (Jørgensen, 1980; and this study).

The mussel-fishery is managed according to a number of regulations. The mussels are dredged by 51 licensed boats smaller than 8 GRT (Gross Registered Tonnage), powered by engines of 175 HP or less. The fishery is

restricted to depths below two or three metres and prohibited in some nature conservation areas resulting in a total fishing area in Limfjorden of around 700 km². Minimum size is 4.5 cm (shell length) but up to 30% of undersized mussels is allowed in the catch. All catches are sorted on land and undersized mussels are relaid at different localities around the sound (Kristensen, 1993; Kristensen and Lassen, 1997).

The landings of mussels have increased from 50 000 tonnes in 1980-1990 to 110 000 tonnes during the last six years. This increase in the landings in the mussel fishery has occurred simultaneously with a decrease in the finfish catches. The high catches and visible environmental effects of the dredges in the form of upwelling of bottom sediment, as well as destruction of bottom animals and eelgrass, has stimulated great interest in the impact of mussel dredging on the ecosystem and on the finfish fishery. No scientific evidence, however, is available to demonstrate a direct interaction

between the increase in the mussel fishery and the decrease in finfish catches. Regardless of these facts strong movements against mussel fishery from other usergroups in Limfjorden, with demands of closing the fishery, have developed during the last five years (Hoffmann, 1994).

In order to elucidate the role of mussels in the ecosystem and the effects of mussel-fishery, absolute estimates of exploited mussel populations is a demand. Mussel abundance can be assessed by different methods. When mussels are living in the littoral and high sublittoral the distribution of mussel beds can be identified by means of aerial photography and sampled directly on the mussel beds (Munch-Petersen and Kristensen, 1989; Munksgaard, 1989; Kristensen, 1995). Alternatively, when mussels live in the sublittoral the animals are sampled randomly from the whole area of interest by dredge (Hoffmann, 1993).

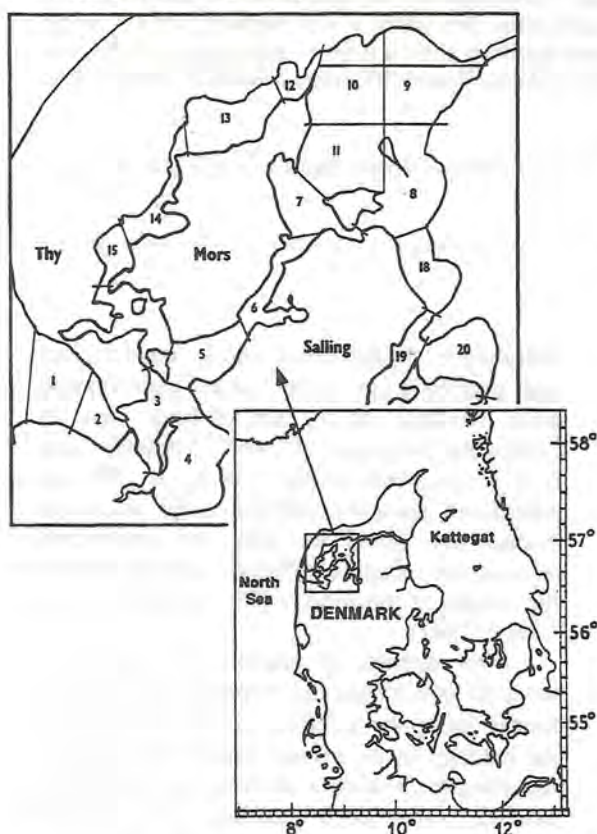


Fig. 1. The study area Limfjorden in the northern part of Denmark with fishery zones 1 to 20. Gray aread indicate areas with oxygen depletion in summer 1994 ($<2 \text{ mg l}^{-1}$ for more than one week)

This study reports a method for assessing blue mussels stocks using a mussel dredge with a known sampling efficiency. Mussel stock estimates from 1993, 1994 and 1995 and calculations of the fraction of the stock removed by the fishery are presented. The effects of the mussel fishery and oxygen depletion on stock size are analysed, and the ecological consequences of mussel dredging are discussed.

Methods

The mussel dredge used in the mussel stock assessment in Limfjorden is a 1:2 scale model of the Dutch model dredges used in the commercial European mussel fishery. The dredge is 120 cm wide and weighs 80 kg. Towing speed was 3.5 knots, and dredging time was one min resulting in hauls of 100 m in length.

Efficiency of the mussel dredge.

The efficiency of the mussel dredge was estimated in nine series of experiments in August 1994 and April 1995. In each series the mussels were sampled in four transects of hundred metres by use of SCUBA and by dredge. Two ropes, equipped with ten steel frames (area=0.28 m^2) fixed on one metre strings in ten metres intervals, were laid on the seafloor. The ropes were placed 4-8 m's apart. Mussels and empty shells in each frame were collected by diver and weights of live mussels determined. Afterwards, two dredge hauls of 100 m length were taken parallel to the ropes. The efficiency of the mussel dredge was expressed as a percentage of the number of mussels caught by the dredge divided by the catch collected by the diver.

Stock size.

The stock size of blue mussels in the central and western part of Limfjorden (Fig. 1) were estimated from data collected on cruises with r/v "Havfisken" in April 1993, 1994 and 1995. The total fishing area in Limfjorden was split into 420 squares of 0.5 nautical square miles each, and one station was randomly selected in each square and dredged. In 1993 and 1994, 362 and 317 of the stations were examined, respectively. In 1995 only 72 stations were selected in the same area as in 1993-94 except in fishery zone 1 and 2 in the most western part of the sound (Fig.

1). On each station a haul of 100 m length in a random direction was taken, and the catch was sorted and the wet weights of live mussels, empty shells and other invertebrates determined.

Since a number of hauls collected during the three years did not contain any mussels the data did not fulfil a normal distribution and stock estimates were thus calculated following the procedure of Pennington (1983). Assuming that the estimated means were approximately normal-distributed, 95% confidence intervals were estimated as 2 S.E. The density of blue mussels (kg/m^2) and the total stock size (tonnes) were calculated for all fishery zones (see below). Furthermore, the total stock was calculated for the whole area in all three years.

Limfjorden is divided into 22 fishery zones (Fig. 1) and the mussel fishermen and the fishery industry report the daily catch weight of mussels caught from each fishery zone to the Ministry of Food, Agriculture and Fisheries. Exploitation rates were calculated for each fishery zone as the annual landing expressed as a percent of a mussel stock in each fishery zone. The effect of the exploitation on the change in stock size were analysed by linear regression for the periods 1993 - 1994 and 1994 - 1995 and the correlation's were tested for significance.

Oxygen depletion

In July and August 1994 extensive oxygen depletion was observed in Limfjorden (Fig. 1). The distribution of oxygen depletion was mapped by the counties surrounding Limfjorden; 30 % of the sound had an oxygen concentration $< 2 \text{ mg l}^{-1}$ for more than one week. In order to analyse the effect of oxygen depletion on blue mussel stocks the fishery zones in Limfjorden were divided into two sections: one suffering from (A) and another (B) not suffering from oxygen depletion during the summer of 1994. The change in stock size between the two sections was tested by Mann-Whitney U-tests on the 1994-1995 data influenced by oxygen depletion and with the 1993-1994 data as controls without oxygen depletion.

Results

Efficiency of the mussel dredge.

The mean efficiency ($\pm 2\text{S.E}$) of the mussel dredge was $17 \pm 5 \%$ ranging from 1 to 43 %

(Fig. 2). The efficiency was correlated significantly with the density estimated by the dredge sampling ($R^2 = 78 \%$, $p < 0.01$), and was fitted with a power function: $\text{Efficiency} = 37 b^{0.71}$ where b is the biomass expressed as catch per m^2 dredged. This function is used below in the calculations of the stock sizes.

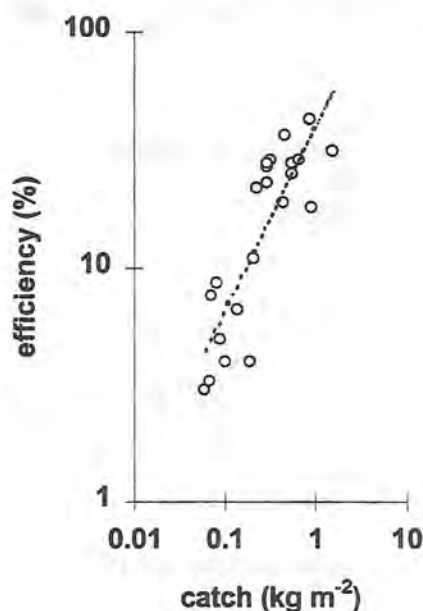


Fig. 2. The efficiency in % (E) of the mussel dredge as a function of the catch of mussels (b). The power function ($E=37 b^{0.71}$) is fitted to data

Stock size estimates of *Mytilus edulis*

In April 1993, 1994 and 1995 the biomass of blue mussels in the fishery zones in Limfjorden was estimated to be 770 000, 616 000, and 494 000 tonnes, respectively. In 1993-94 the mean exploitation rate was 14 %, ranging from 0 to 31 %. The exploitation rate was significantly and negatively correlated ($p < 0.05$) with the change in stock size (Fig. 3). In 1994-95 the mean exploitation rate was 15 %, ranging from 0 to 38 %. No significant correlation ($p > 0.05$) between the exploitation rate and the change in stock size was observed (Fig. 3).

Effect of oxygen depletion on stock size

The change in mussel stocks between 1994 and 1995 was related to the distribution of oxygen depletion in summer 1994 (Fig. 1). Each fishery zone was categorised as suffering from (A) or not suffering from (B) oxygen depletion. The

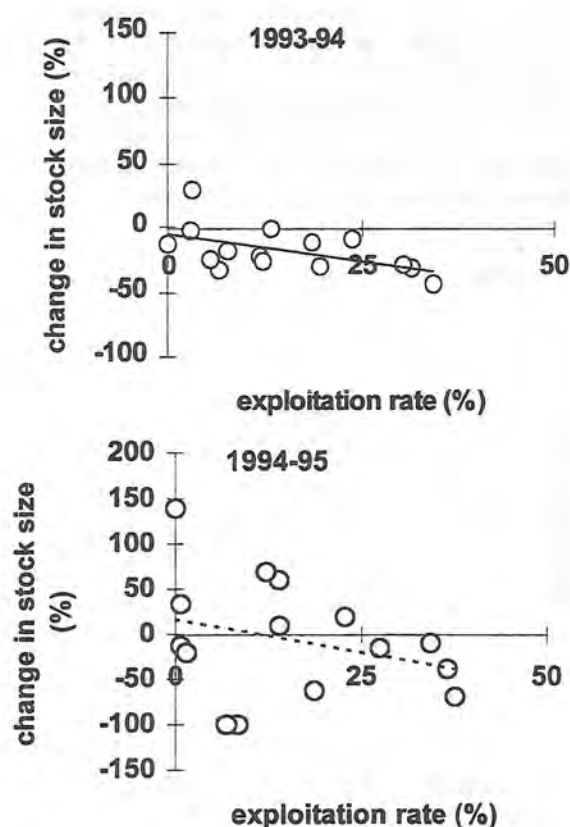


Fig. 3. The change in stock size in each fishery zone as a function of the exploitation rate estimates for the same zones in the periods 1993-94, and 1994-95. In 1993-94 the change in stock size was significantly correlated to the exploitation rates ($R^2=0.34$, $p<0.05$), whereas no significant correlation's were observed in 1994-94 ($R^2=0.09$, $p>0.05$).

zones exposed to oxygen depletion had a significant reduction (Mann-Whitney, $p<0.05$) in biomass compared to the stable zones. In 1993-1994 no significant difference ($p>0.05$) was observed between the areas with or without oxygen depletion in 1994 (Fig. 4).

Increase in the stock size (± 2 .S.E) between 1994 and 1995 in fishery zones without oxygen deficiency was 46 ± 60 % compared to a reduction of 33 ± 38 % in the fishery zones exposed to oxygen depletion (Fig. 4). The total reduction in stock size in the fishery zones with oxygen depletion was 131 000 tonnes compared to an increase of 36 000 ton in the zones without oxygen depletion.

Discussion

Allen and Cranfield (1976) suggested that the dredging process can be separated into three stages. Just after contact with the bottom the dredge has a high efficiency, afterwards the dredge starts to fill and the efficiency decreases as the dredge becomes filled. At the end of the haul the dredge is totally full and the bivalves are just pushed aside. McLoughlin *et al.* (1991) reviewed the efficiency of different types of dredges primarily used in the scallop industries. For all dredges the efficiencies ranged from 5 to 35 %. In the reviewed studies the efficiencies are not correlated to the density of the bivalves on the bottom: In this study the efficiency ranged between 1 to 43%, and was positively correlated to the mussel biomass.

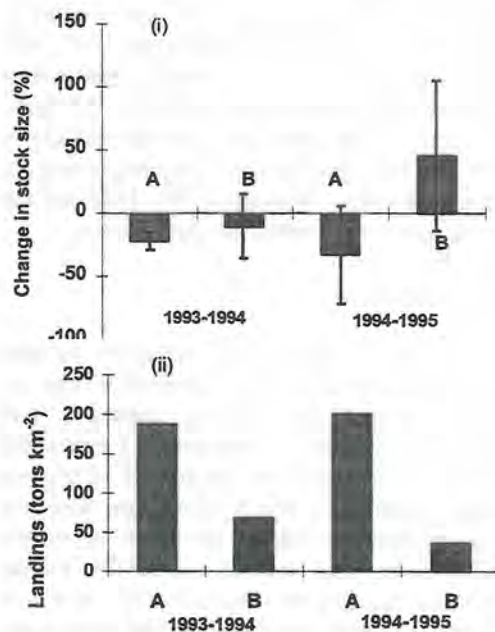


Fig. 4. The change in stock size (i) and landings in fishery zones (ii) in 1993-94 and 1994-95. (A) represents the fishery zones, where oxygen concentrations $< 2 \text{ mg l}^{-1}$ were recorded for more than one week in the summer of 1994, and (B) represent the section of fishery zones not influenced by low oxygen concentrations in summer 1994. In 1994-95 30 % of the area was affected by oxygen depletion, whereas 1993-94 serves as a control situation with apparently no oxygen depletion periods.

Bluemussel stocks, Limfjorden 1993-1995

Fishery zone	1 + 2	3	4	5	6	7	8	9	10	11	13	14	15	18	19	20	sum
1993																	
n	17	24	16	23	16	14	47	14	29	45	24	14	12	21	19	27	362
mean density (kg/m2)	0.52	0.48	0.69	0.63	0.87	0.96	1.26	1.51	1.47	1.72	1.29	1.25	1.45	0.68	1.65	1.36	
2 S.E./m %	40	49	36	29	31	24	27	23	40	22	29	56	46	55	19	25	
stock (tonnes)	43212	18845	36324	26429	19413	28663	89376	47001	92310	118739	64753	24929	27074	23437	46136	63978	770618
2 S.E.	17240	9240	12973	7613	6082	6949	24296	10797	36875	26008	19029	13925	12375	12872	8873	15977	241125
1994																	
n	10	23	24	24	14	10	39	13	18	19	30	12	13	22	20	26	317
mean density (kg/m2)	0.31	0.62	0.56	0.55	0.58	0.66	0.87	1.16	1.44	1.27	0.96	1.13	1.29	0.38	1.18	1.34	
2 S.E./m %	76	41	37	38	39	40	29	29	35	22	37	46	42	55	24	17	
stock (tonnes)	26217	24344	29865	22988	12987	19677	61803	36248	89983	87448	48165	22517	23983	13182	32984	63137	615527
2 S.E.	19823	9912	11037	8817	5075	7831	17942	10375	31623	19445	17938	10290	10136	7201	7799	10703	205946
1995																	
n		4	6	6	3	2	8	3	7	10	5	3	3	4	4	5	73
mean density (kg/m2)		0.82	0.49	1.32	0.69	1.05	0.95	1.05	1.14	1.07	0.00	0.70	2.18	0.00	0.36	0.50	
2 S.E./m %		74	122	57	101	16	38	21	62	44	0	52	26	0	110	80	
stock (tonnes)		32469	26075	55020	15467	31447	67386	32688	71549	73844	0	13853	40543	0	10123	23575	494039
2 S.E.		24003	31862	31189	15690	5033	25319	7006	44652	32582	0	7155	10341	0	11157	18817	264806
area of zone (km ²)	83	39	53	42	22	30	71	31	63	69	50	20	19	35	28	47	702
landings 93-94 (tonnes)	256	604	2760	0	1287	9000	17532	5467	2690	14376	3612	5948	4987	8044	14073	8463	99100
landings 94-95 (tonnes)	0	173	202	8	2957	2712	8535	12399	1355	24044	3962	8228	2884	895	12403	11691	92447
exploitation rate 1993-94 (%)	1	3	8	0	7	31	20	12	3	12	6	24	18	34	31	13	
exploitation rate 1994-95 (%)	0	1	1	0	23	14	14	34	2	27	8	37	12	7	38	19	

Table 1. Mean density and stock size in the fishery zones 1 to 20 in 1993-95. In the lower part of the table: The area of the zones, the reported landings, and the exploitation rate in 1993-94 and 1994-95. In the right part of the table: Number of hauls (n), the total stock size in 1993-95, the total landings in 1993-94 and 1994-95.

Blue mussels dominate the suspension-feeding benthic community in Limfjorden and can control the phytoplankton biomass in some areas (Cloern, 1982; Møhlenberg, 1995). A removal or decrease in the mussel population could thus reduce the filtration capacity of the mussel populations until new recruitment. Officer *et al.* (1982) discussed the importance of mussels in controlling the phytoplankton biomass. They listed important criteria for benthic filter feeding populations in controlling the phytoplankton population and these included shallow water, a large benthic filter feeding population, poor hydrodynamic exchange, adequate nutrient supplies and a constant or low concentration of phytoplankton and modest bloom periods. All criteria are valid for at least some parts of Limfjorden: The mean depth in the sound is 7 m and the population of blue mussels is large with other suspension feeding organisms present such as cockles and ascidians in the western part. Furthermore, Limfjorden consists of several connected enclosures and variations in the sea-level and water exchange is small; nutrient rich runoff from farmland is present all around the sound sustaining a high primary production (Jørgensen, 1980).

Stratification and insufficient water mixing is reported to increase the phytoplankton-concentration caused by a low vertical flux of phytoplankton from the water column to the filtering benthic community, whereas in well mixed conditions the benthic suspension feeders may control the phytoplankton population (Cloern, 1982, 1991; Møhlenberg, 1995). Removal of mussels by fishery, as well as an effect of oxygen deficiency or biological interactions may reduce the stock of suspension feeding organisms in Limfjorden resulting in periodically inadequate control of the phytoplankton blooms. In 1993-94 and 1994-95 respectively 14 % and 15 % of the mussel population was taken away by fishery. In 1993-94 the exploitation of the mussel stock was correlated with a reduction of the stock size, indicating that the mussel fishery in Limfjorden in 1993 to 1994 strongly affected the size of the mussel population.

In those fishery zones where oxygen depletion was observed the mussel stocks were reduced by 33 % compared to a 46 % increase in stock sizes in areas without oxygen depletion. In terms of biomass the stocks in areas with oxygen depletion were reduced by 131 000

tonnes, equivalent to more than one year of landings of mussels. Converting the biomass from wetweight to nitrogen and phosphorus content by use of Redfield's ratio (Redfield, 1958) resulted in a release of approximately 150 tonnes of phosphorus and 1 000 tonnes of nitrogen to the water column. These amounts correspond to 25 % and 5 % of the annual discharge of phosphorus and nitrogen, respectively, from land to the whole waterbody.

The environmental effects of resuspension of bottom material a mussel fishery through dredging, and the subsequently release of nutrients and decrease in oxygen content was investigated in field experiments by Riemann & Hoffmann (1991) and Dyekjær *et al.* (1995). Riemann & Hoffmann (1991) observed a significant increase in suspended material corresponding to 1,47 kg sediment per m² dredged which lasted for 30-60 minutes. The suspension was coupled to a small decrease in the oxygen concentration in the water column. They concluded that oxygenation of anaerobic sediment and reduced chemical compounds reduced the oxygen concentration. In addition, they observed an increase in the amount of silicate. No significant increase in the concentration of nitrate and phosphate was observed. Dyekjær *et al.* (1995) observed a suspension of material corresponding to 2 kg sediment m⁻²-dredged. On the basis of knowledge of the total mussel fishery in the sound they estimated a yearly release of nitrogen and phosphorus from the dredges to be less than 1% of the external load. They concluded that the total annual release of nutrients caused by dredging has little effect on the overall eutrophication status of the sound.

The mussel fishery in Limfjorden takes place in all areas of the sound except from a few enclosures where fishing with moving gear is prohibited. In future regulation of the fishery, it has to be considered to what extent dredging should be increased in areas frequently exposed to oxygen depletion and to what extent dredging should be reduced in stable areas. Such a regulation in the fishery would reduce the biomass of mussels and reduce the release of nutrients in case of oxygen depletion and mass mortality of mussels. Furthermore, areas with stable populations of mussels would be exploited at a lower rate and evolve a constant high filtration capacity.

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